The Reproductive Ecology of Vascular Plants on Subantarctic Macquarie Island

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Submitted in fulfillment of the requirements of Doctor of Philosophy

School of Plant Science

University of Tasmania (November 2005)

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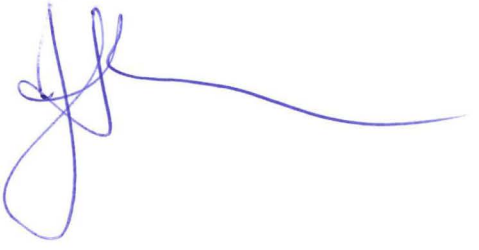

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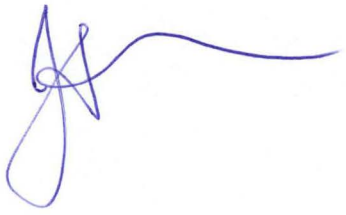

Acknowledgements

There are many people who have played a role in my work through a variety of ways; educational, physical, financial, logistical, and emotional. In summary:

Dr Dana Bergstrom for introducing me to the subantarctic and seeing that I was a suitable person for island life. For her continued passion for subantarctic ecology and most importantly her ongoing support and encouragement and allowing me to 'go south' again and again. For many years ago having a poster on her door 'Women in Antarctica' guaranteed to capture the attention of any wayward young girl.

Dr Mark Hovenden for being an amazingly patient supervisor. For his ability to give sampling advice over the phone without being able to see the plants or field sites. For encouraging me to *pursue* my writing skills. For getting excited about my work, and for being a very sound and enthusiastic ecologist.

Dr Jenny Scott for stimulating discussion, having copies of archaic old journals, and reminding me of the values of long term monitoring. And for hating rabbits.

Nigel Brothers for discussion whilst in the field, having an amazing memory and having a different slant and always thinking at the island scale.

Dr Craig Tweedie who taught me how to do fieldwork in the subantarctic, his encouragement and feedback, inspiring me to work hard and always reminding me to think about 'the big picture'.

For their knowledge and helpful discussion: Dr Rod Seppelt, Dr Patricia Selkirk, Dr Niek Gremmen, Prof. Steven Chown, Penny Greenslade, Geoff Copson

Many people assisted me with my field work, in trying conditions: John Lynn, Jean Osanz, Louise Crossley, Keith Springer, Matthew Pauza, Ryan Munro, Matthew Webb.

Mark Geyle & Robb Clifton for their logistic support (no pack too heavy) & friendship, Sue Robinson just for being a sub-antarctic she-hero.

Tore Pedersen for being my mountain and lab companion, a Weather Station doctor, and always being calm

Rachael Alderman for going to Macquarie I. and bring reality to my island days. For thinking it's totally normal to dance around Bauer Bay beach in a bikini.

To my brother Brendan, for phone workshops and understanding what it means to write a PhD, and for being a great friend.

To my parents for instilling in me that education comes first, for encouraging me in all things I choose to do. For their support and ongoing interest in my work, and thinking it fine that I stay a student for over a decade.

Wieslawa Misiak, from the herbfield to the office, from Christchurch to Adelaide... always understanding everything from nil germination to concrete data. Thanks Petal!

Finally to Aleks Terauds ....Thank you for everything - being an athlete, a genius, an editor, a counsellor, a budding botanist. For teaching me how to cross a frozen skree slope and sharing the island with me. Thank you infinitely for always being there, then and now.

Abstract

Southern Ocean islands have long been sites of scientific interest, due to their isolation, climate, geology and biology. This study investigated reproductive ecology of vascular plants on subantarctic Macquarie I. The persistence of plant species in a community relies on life history strategies which ensure population growth and sustainability. This can be via either vegetative or sexual reproduction. Many studies have shown that for alpine and high latitude plants sexual reproduction is not an important life history trait.

The study identified that 26 species flowered, 22 dispersed seed and 12 produced seedlings over the study period on Macquarie I. This represents 72%, 61% and 33% of the angiosperm flora of the island, respectively. There was a strong seasonality with almost all species flowering and fruiting in spring and summer. Overall sexual reproduction coincided with an increase in day length in summer. Seed rain of several plant communities was measured across eight sites of differing environments. At most sites seed rain was representative of standing vegetation, with the most widespread and abundant species on the island being the most widespread and abundant species present in the seed rain. The study has shown that several species (particularly *Pleurophyllum hookeri* and *Stilbocarpa polaris*) produced large numbers of seeds (over 13, 300 seeds m^{-2}) which are greater seed rain densities than previously recorded in arctic and alpine studies.

Both species of large leaved megaherb (*P. hookeri* and *S. polaris*) are abundant on the island. *S. polaris and P. hookeri* allocated resources similarly as both species were found to allocate over 50 % of their total biomass to leaf tissue and a substantial proportion of biomass (20+%) to sexual reproduction. The study identified that seed germination occurred for megaherbs across a range of altitudes. Seedling densities recorded for both species were extremely high (up to 10, 000 m^2). Despite high seedling mortality during the study many seedling were observed to survive to become juvenile plants. *P. hookeri* population demography was investigated across four different populations. All were found to be dominated by large old plants. Despite some demographic variation between populations, seedlings were recruited into the population at most sites. Alien species were found to have deleterious impacts on megaherb species through seed predation, seedling herbivory, and site disturbance.

This study has shown that plants on subantarctic Macquarie I. allocated considerable resources to sexual reproduction which is an important plant life history strategy for plants growing in this environment.

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Chapter 1 - Introduction

Subantarctic Islands

The terrestrial subantarctic region consists of the oceanic islands that lie in the Southern Ocean, spanning a latitudinal range of approximately 45°S to 55°S. These islands are unusual as they are generally small, extremely isolated from each other and continental landmasses and have low mean summer temperatures. Regarded as being of considerable biological and conservation importance, they form the nesting grounds of a significant portion of the world's procellariiform species (petrels and albatrosses) (Chown et al. 1998a) as they are the only ice-free land available in the Southern Ocean. Many species of penguins (sphenisciformes) also using them as breeding platforms (Bergstrom and Chown 1999). Additionally these islands are home to a variety of endemic plant species (Greene and Walton 1975; Gremmen 1981; Hnatiuk 1993) and as stated by (Chown et al. 1998b) 'because of the paucity of land in this region, provide the only examples of mid-to high latitude southern terrestrial biomes'.

The region's climate is a prevailing oceanic, or maritime climate, meaning the insular temperature regimes follow that of the surrounding ocean very closely, rather than diurnal or annual cycles (Huntley 1971). Thus the resulting climate can best be described as cold, wet and windy with minimal annual temperature variation. Due to the latitude, day length varies considerably over the year, from about 7 hours in June to over 16 hours in December..

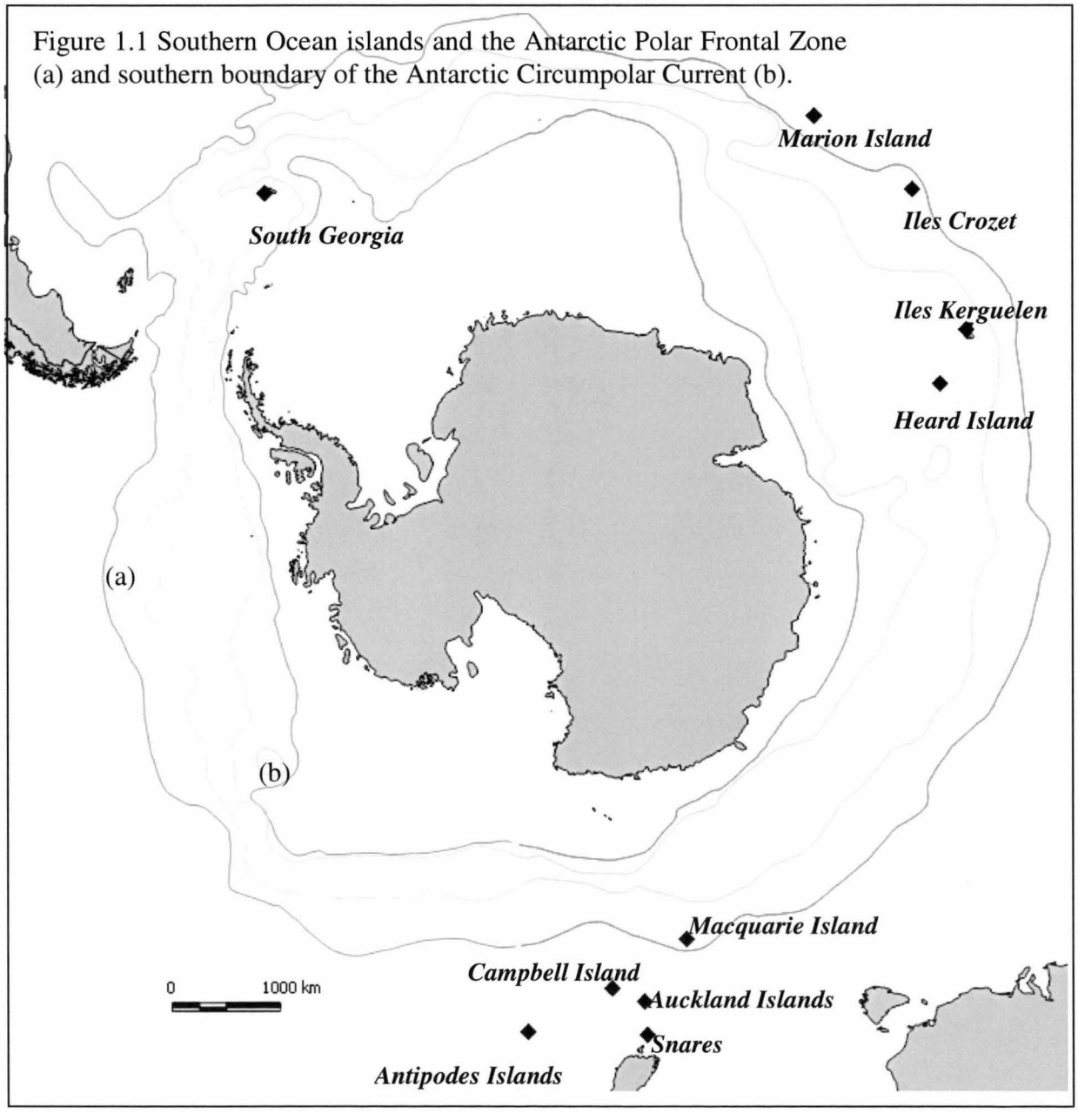
The subantarctic can be further sub-divided on climatic and glaciological criteria (Lewis-Smith 1984). The Antarctic Polar Frontal Zone (APFZ), is an oceanic front where cold Antarctic waters sink below a warmer surface layer. The APFZ strongly influences the Southern Ocean and consequently those islands which occur in this region and the islands' climates. Islands that are north of the (APFZ), such as Macquarie I., which are ice-free with no permanent snowfields, are referred to as the cool subantarctic (Lewis-Smith 1984). Those islands which lie to the south, such as Heard I. and South Georgia, are heavily glaciated, and described as cold subantarctic (Lewis-Smith 1984). An island's elevation also influences the extent of snow cover and glaciation.

It is difficult to list the islands which are considered subantarctic, with opinions being as numerous as researchers. There is no debate regarding the subantarctic status of South Georgia, Îles Crozet, Îles Kerguelen, Heard and MacDonald Is., Marion and Prince Edward Is., and Macquarie I. However, there is much discussion as to whether Gough I., Islas Diego Ramirez and Campbell I. are truly subantarctic islands. Wace (1960), Huntley (1971), Lewis-Smith (1984), Walton (1985) and Selkirk (1992) rejected the inclusion of these islands into the subantarctic zone, as they have summer temperatures warm enough to support arborescent plants and cushion bogs. These researchers classify such islands as cold temperate.

With a mean summer temperature of 9.0°C Campbell I. is biogeographically very similar to Macquarie I. Other researchers (Meurk 1977; Meurk et al. 1994b; Mitchell et al. 1999; Nicholls and Rapson 1999) considered Campbell I. to be subantarctic.

Bergstrom and Chown (1999) pointed out that these ecological classification schemes served more to emphasise the differences between islands than their overall similarity. (Chown et al. 1998b; Chown et al. 2001). Chown and colleagues (1998b, 2001) overcome the issues of island classification by referring to all the islands as Southern Ocean islands, which acknowledges that there are no true boundaries and the biota of all islands reflect varying environmental gradients across the region. This thesis shall refer to all islands as Southern Ocean islands (Figure 1.1) and refer to the Macquarie I. environment as subantarctic.

Figure 1.1 Southern Ocean islands and the Antarctic Polar Frontal Zone (a) and southern boundary of the Antarctic Circumpolar Current (b).



Subantarctic Vegetation

As discussed there are many definitions of the 'subantarctic' region. Generally, the subantarctic islands (as defined above) are biologically challenging, additionally the islands are geographically isolated as a result these islands support an impoverished flora. Vascular plant species richness for each island can be explained by island area and island temperature (Chown et al. 1998b). No trees or shrubs grow on the 'true' subantarctic islands, with the vascular flora comprising grasses, herbs and ferns. Bryophytes and lichens are more diverse and dominate the region's flora. Collectively across these islands are approximately 24 graminoids, 32 herbs, 16 pteridophytes and numerous bryophytes (250+), liverworts (150+) and lichens (300+) (Lewis-Smith 1984). As discussed Campbell I. has been considered both subantarctic and cold temperate. The island supports 140 vascular plant species, of which seven are woody species which create dwarf forests (up to 5m high) and shrub associations (Wilmshurst et al. 2004). Eighty five cryptogammic species have been recorded (Meurk et al. 1994b) for the island. Macquarie I. has the strongest biogeographic affinity to Campbell I.

Only two native (*Deschampsia antarctica*, *Colobanthus quitnesis*) and two alien (*Poa anuua* and *Poa pratensis*) vascular plant species have been found growing in maritime Antarctica (Frenot et al. 2005). As such the subantarctic islands represent the southern limit of many vascular plant families and genera, as well as relatively complex vascular plant dominated plant communities. Several species are restricted to the region, but few are endemic to individual islands. The vegetation patterns of these Southern Ocean islands have a circumpolar unity (Walton 1985; Meurk et al. 1994a; Meurk et al. 1994b) with species richness being influenced by latitude, isolation and

land size (Chown et al. 1998b; Greve et al. 2005). As this thesis deals with flowering and sexual reproduction the term vegetation will largely refer to vascular plant communities.

Macquarie Island

Macquarie Island is approximately 1500 km southeast of Australia in the Southern Ocean. It's nearest neighbouring land mass is the Auckland Is. group approximately 600 km away. Of all the subantarctic islands Macquarie I. at 54°30'S, 158°57'E, occurs at one of the most southerly latitudes, second only to South Georgia (Figure 1.1). Macquarie I. is one of the younger Southern Ocean islands (Selkirk et al. 1990a). Being the one of the lowest in altitude (Plate 1.1a &b) of all the subantarctic islands it has no glaciers or permanent snow. The island is 12 870 ha in area. The island has been aged between 600, 00 and 700, 000 years old (Adamson et al 1995; 1996).

Vegetation

There are 46 vascular plants recorded for Macquarie I. The island has a biogeographic affinity with Australasia (Walton 1985), and more specifically shares 31 species (67%) with Campbell and Auckland Is. (Selkirk et al. 1990b; Greve et al. 2005). There are species which also occur outside of the subantarctic, as far north as Tierra del Fuego (3 species), Australia (9 species) and one indigenous species also occurs in the northern hemisphere. In sheltered sites, plant productivity and rates of peat accumulation can be very high (Jenkin and Ashton 1970; Jenkin 1975; Selkirk-Bell 2000; Tweedie 2000). The flora of Macquarie I. comprises grasses, sedges and rushes, herbs, megaherbs and bryophytes (Selkirk et al. 1990b; Hnatiuk 1993). Of the

bryophytes, 84 mosses have been identified and with a further four collected but unidentified (Seppelt 2004).

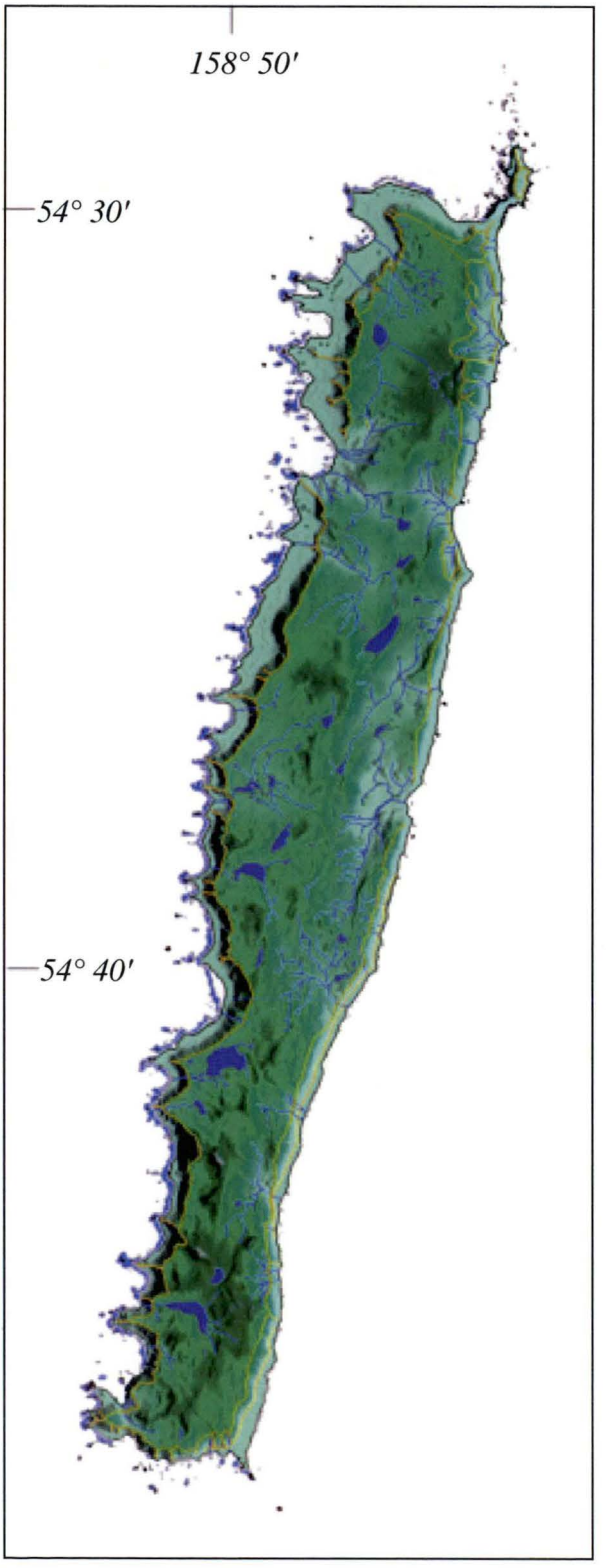


Plate 1.1a Relief map of Macquarie I. Data courtesy of the Australian Antarctic Datacentre and NASA

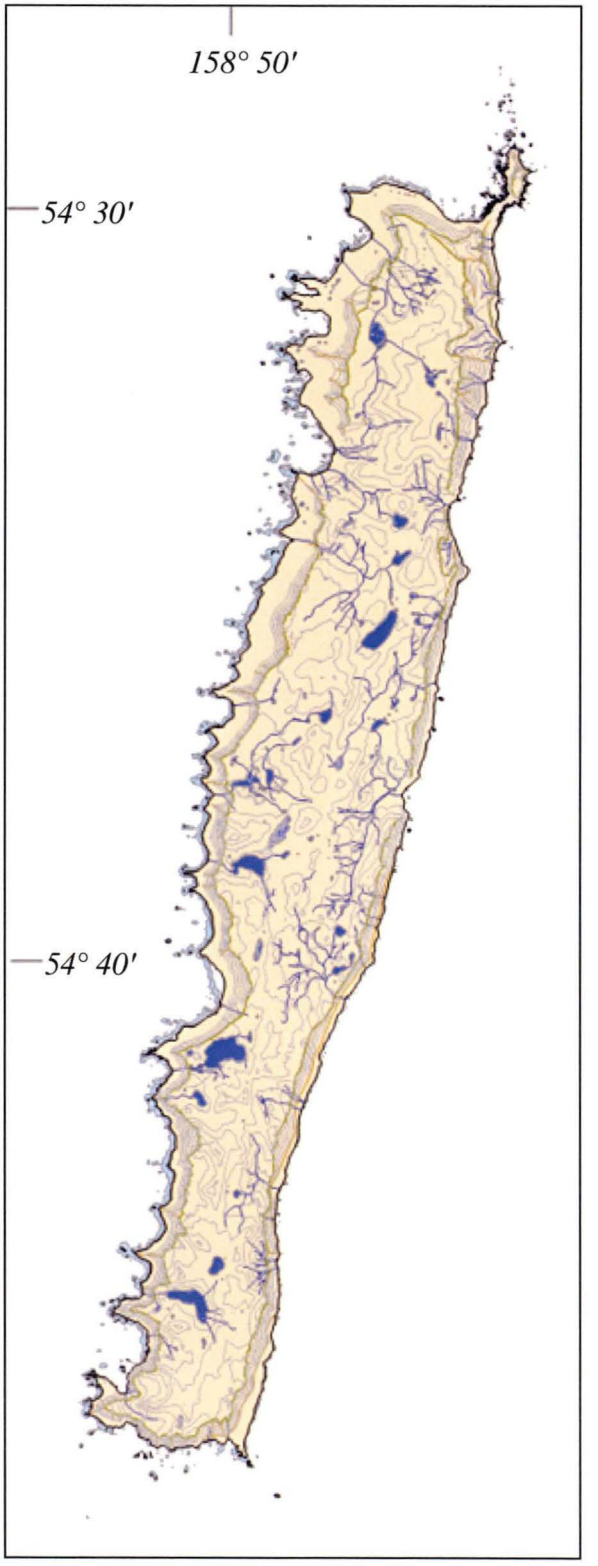


Plate 1.1b Topographic map Macquarie I. (50 m intervals). Data courtesy of the Australian Antarctic Datacentre and NASA

There are thought to be over 50 hepatics and 100 lichen species on Macquarie I. (Selkirk et al. 1990b). The three largest species of flowering plants (*Poa foliosa*, *Stilbocarpa polaris*, *Pleurophyllum hookeri*) all dominate the coastal slopes of the island. These species are also found on the Snares, Auckland and Campbell Is.

Vegetation communities

Taylor (1955) defined five major vegetation groups on Macquarie Island: feldmark, bog, fen, herbfield, grassland. Within these, he described species alliances and associations. Selkirk et al. (1990b) expanded on Taylor's scheme, providing the most recent classification to date. The vegetation communities defined by Selkirk et al. (1990b) are: tall tussock grassland, short grassland, fernbrake community, mire, feldmark and herbfield. The island's vegetation has been mapped based on general vegetation types (Selkirk and Adamson 1998); however, a review of the island's vegetation classification and a more detailed vegetation map are needed. A brief description is given of the major communities referred to by Selkirk et al. (1990b).

Tall tussock grasslands are dominated by *Poa foliosa* tussocks and occur as open or closed vegetation predominantly on steep coastal slopes (see Plate 1.2), beach margins and coastal terraces where the water table is not at the surface. *Poa foliosa* can grow to heights of up to 2m, forming peaty pedestals that vary in density. Where dense, few other vascular plants grow, however, some small herbs and bryophytes do occur in canopy gaps. In areas where tussocks are more widely spaced, the megaherb *Stilbocarpa polaris* can co-dominate. In sheltered, low altitude sites, both species are highly productive and can form dense canopies over 1m high. At more exposed, higher

altitude sites, both species adopt a non-pedestal form and are less productive (Jenkin 1972; Scott 1985; Scott 1995).

Plate 1.2 Tall tussock grasslands dominated by *Poa foliosa*.

Herbfields occur on slopes and flats subject to moderate winds, in areas where wind exposure is low such as valleys (Selkirk et al.1990b) (see Plate 1.3D). They also occur on upper coastal slopes, which are not steep. Taylor (1955) and Selkirk et al. (1990b) each provided definitions of herbfields. Selkirk et al. (1990b) distinguished three types of upland herbfield as being dominated by *Acaena* spp., by *Pleurophyllum hookeri* and *Stilbocarpa polaris* (see Plate 1.3A), or by *P. hookeri* and *Azorella macquariensis* (see Plate 1.3B). These definitions were applicable to this study, however, the term herbfield has also been applied to communities which are dominated by *S. polaris* and with limited (<10%) cover of *Poa foliosa,* such as occur on coastal slopes or uplands. *S.*

polaris herbfields do not occur on the island plateau, while *P. hookeri* herbfields do. Low altitude *P. hookeri* herbfields are very productive (Jenkin 1972).

Rabbits have greatly reduced the cover of *P. hookeri* herbfields since their introduction approximately 150 years ago (Copson 1984). Peat cores collected in areas now supporting short grassland suggest such areas once supported herbfields in the past, and their removal by rabbits has lead to a reduction in the rate of peat formation within these areas (Selkirk-Bell 2000).

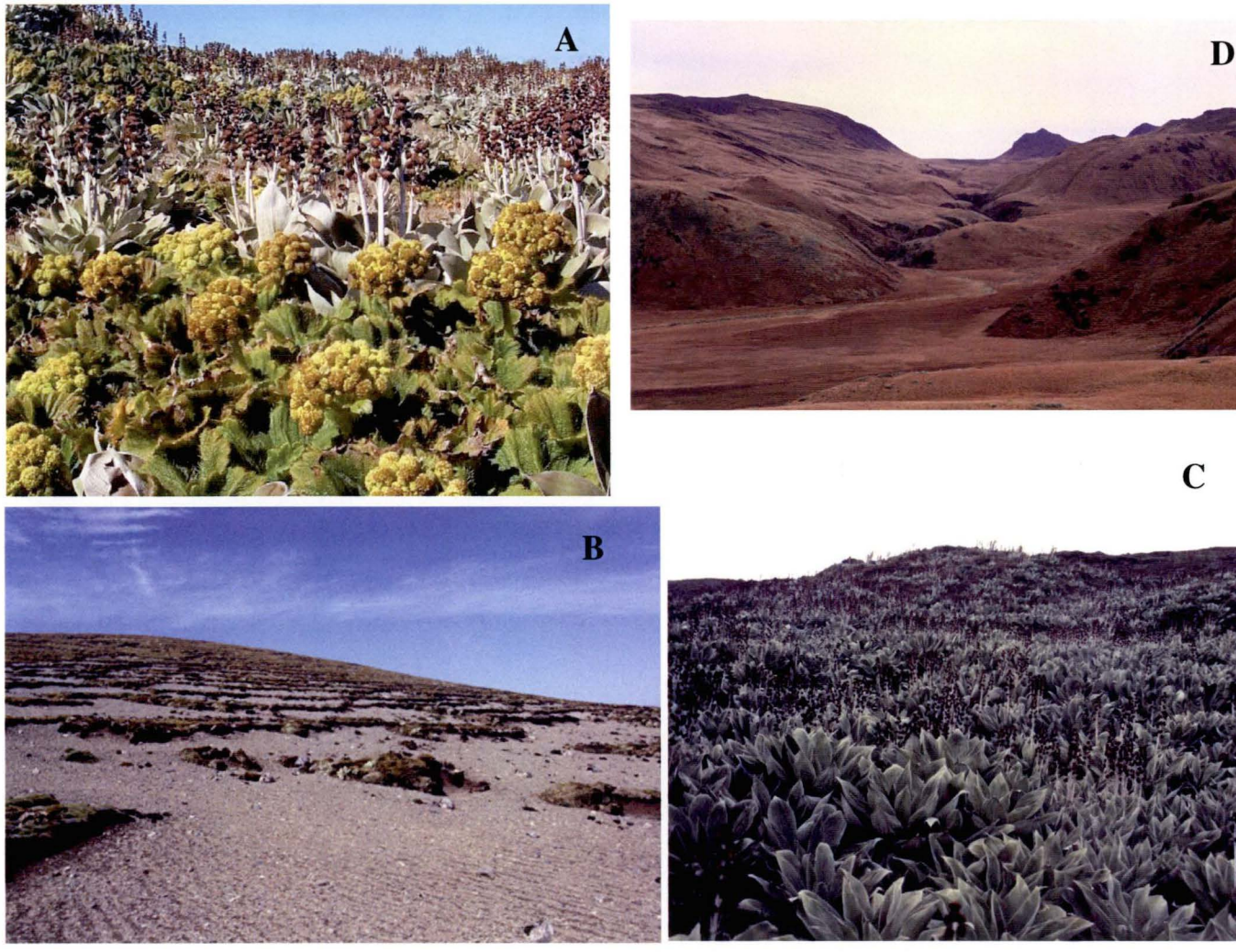


Plate 1.3 **A** Herbfield co-dominated by *S. polaris* and *P. hookeri*. **B** Short grassland covered slopes in winter. **C** Feldmark community. **D** Herbfield dominated by *P. hookeri*.

Short grasslands cover a large area of the island, usually occurring on upland coastal slopes or in upland valleys and sheltered slopes (see Plate 1.3D). The abundance of this community is the result of selective grazing by rabbits and it can be regarded as a subclimax community following grazing of tall tussock grasslands or herbfields (Selkirk et al. 1990b). Short grasslands are dominated by the grasses *Festuca contracta* and *Agrostis magellenica*, and the small sedge *Luzula crinita*. In these communities, vegetation cover is extensive, usually 100% surface cover, and despite its low stature, generally has a dense understorey of bryophytes.

In exposed sites on mineral soils, as is common on the upland plateau, feldmark communities prevail. Feldmark is typified by low vegetation cover attributed to skeletal low nutrient soils and harsh environmental conditions, being high and exposed. Amongst the vegetation are bare gravel patches. Lichens often grow in these bare patches and bind the soil and gravel (Selkirk et al. 1990b). Feldmark communities are dominated by bryophytes, in particular *Racomitrium crispulum* and *Ditrichum strictum*. *Azorella macquarienesis* is the only vascular plant that ever dominates feldmark and is often a major structural component, upon which other plants colonise. Structure is complex and variable, with *Pleurophyllum hookeri* common in more sheltered areas. In this study, these areas are referred to as *Azorella –P. hookeri* dominated feldmark.

Mire communities occur where the water table is high and drainage poor, which is common on the raised coastal terraces of the north west and west coast. These communities are dominated by *Juncus scheuchzeriodes*, *Montia fontana*, *Ranunculus crassipes*, *Agrostis magellanica* with several other small herbs restricted to these

waterlogged communities. Bryophytes, such as *Breutelia pendula*, *Bryum laevigatum* and *Riccardia cochleate*, are also a major component of mire communities.

Unlike other subantarctic islands, fernbrake communities are not a major component of the island's vegetation occurring in a few sheltered patches along the eastern side of the island.

Vascular Plant Species of Macquarie I.

The vascular plants can be grouped or classified in many different ways, for example by taxa or distribution or abundance. Below they have been grouped according to functional groups. This has been done to give an overview of the major components of the island's vegetation without going into detailed species descriptions. In some instances, these groups have a taxonomic affinity, but overall they group plants of similar growth habit and function.

Ferns and fern allies

There are five species of pteridopytes on Macquarie I.; three species of fern, one filmy fern and one lycopod have been recorded. The ferns *Polystichum vestitum*, *Blechnum penna-marina*, *Grammitis poeppigiana*, are each from a different family. They are not widespread on the island. *P. vestitum* occurs on low altitude east coast slopes, often in the vicinity of penguin colonies. *B. penna-marina* occurs in short grasslands at mid-altitudes. *Grammitis poeppigiana* is restricted to feldmark community where it grows amongst bryophytes and cushion plants. The filmy fern, *Hymenophyllum falklandicum,* and the lycopod, *Lycopodium australiana,* are found in upland areas of feldmark, and during the study both were found to be locally rare. Rabbit grazing has

negatively impacted on *L. australiana,* and therefore it may have had a wider distribution prior to rabbit introduction.

Plate 1.4a *Blechnum penna marina*, each frond is 15 cm

Plate 1.4b *Polystichum vestitum*, each frond is 50cm.

Grasses

Of the flowering plant species that occur on Macquarie I., approximately one quarter are grasses (family Poaceae) varying in stature and habit. The tussock–forming *Poa foliosa* forms thick pedestals and stands up to 1.8 m high. It is the major structural component of tall tussock grasslands, which cover the island's coastal slopes. *Poa foliosa* constitutes a major component of the island's vegetation biomass and is widespread (Copson 1984) however, while it is visually apparent this has never been quantified with detailed mapping. The other large grass, *Poa cookii*, is common in west coast bays and also occurs in several locations on the east coast, although its distribution is typically restricted to the periphery of penguin colonies. The short tussock grasses *Agrostis magellanica* and *Festuca contracta*, are abundant and

widespread. These species dominate in short grasslands, but also occur in feldmark and mire communities. *Deschampsia chapmanii* and *Deschampsia caespitosa* are not common, and are found mainly in wet short grasslands. The low turf-like *Puccinellia macquariensis* is an endemic species restricted to coastal rockstacks, where it grows in conjunction with the small cushion plant, *Colobanthus muscoides*. These habitats are subject to salt spray and manuring by numerous penguins, cormorants and seals. *Poa litorosa* is rare on the island, occurring only in two populations, in the north west (Handspike Corner) and the south (Petrel Peak) (Bergstrom et al. in press). The restricted distribution of this species is discussed later in this chapter in relation to seed dispersal

Sedges and Rushes

There are six species of sedges and rushes (families Cyperaceae and Juncaceae). *Luzula crinita* is very common and widespread across the island. *Juncus scheuzerioides, Carex trifida, Isolepis aucklandica* are restricted to waterlogged mire communities over a range of altitudes. *Uncinia hookeri* occurs in short grasslands, while *Uncinia divaricata* can be found in feldmark communities.

Megaherbs

In addition to the 14 herb species (below), there are two large herbs species, referred to as megaherbs (Hooker 1844) *Pleurophyllum hookeri* (up to 85 cm high) and *Stilbocarpa polaris* (up to 1.7 m high) are the major structural component in herbfield communities. They are extremely productive species which bear many large inflorescences. Both have large leaves and rhizomes in comparison to other subantarctic plants. This makes them particularly attractive to rabbits as a food source.

Small Herbs

The 14 small herb species (from eleven different families) on the island are all low in stature, being less than 20 cm high. Most species are perennial. The rosaceous *Acaena magellanica* and *Acaena minor* are prostrate creepers with suffrutescent stems, with *A. magellanica* being semi-deciduous. Both species are widespread, occurring in all vegetation types. The small herbs *Montia fontana* and *Callitriche antarctica* occur in eutrophic environments, such as nutrient-rich wet, muddy wallows, formed by moulting elephant seals as well as in mire communities. The brassica *Cardamine corymbosa* forms small rosettes, no taller than 10 cm in height or width. *Montia fontana, C. antartica, C. corymbosa* are all widespread across the island. *Ranunculus crassipes* also occurs across a range of communities, thriving in waterlogged areas, where it forms thick mats with leaves up to 5 cm in diameter.

Plate 1.5 *Luzula crinita* flowers

Plate 1.6 *Ranunculus crassipes* flower

Epilobium pedunculare and *Epilobium brunnescens* are small rhizomatous herbs that can form extensive mats. These two species, along with *R. crassipes*, occur in most communities over a wide altitudinal range, and are pioneer species, colonising recently disturbed areas or sand blows. *Stellaria parviflora*, a chickweed (with leaves <1 cm in diameter) possesses a creeping rhizomatous habit and its small size often makes it difficult to locate. The species is most common in short grasslands but can sometimes occurs in feldmark communities. *Leptinella plumosa* is a small coastal herb. It grows up to 20cm high in dense rhizomatous mats. In beach sand deposits *L. plumosa* can also grow as individual rosettes. *Crassula moschata* is restricted to coastal areas and grows on rocks or sand where it co-occurs with *Colobanthus muscoides*. C*olobanthus affinis* and *Colobanthus apetalus* form dense mats which can be described as cushions, although they are not true tight cushions. Both species are restricted to wet areas and are common in mire communities and can only be differentiated by their flower anatomy. For this reason during the study they are often jointly referred to as *Colobanthus* spp.

*Nematocerus dienema (*previously known as *Corybas dienemus)* a small orchid standing approximately 2 cm high, is endemic to Macquarie I. The only orchid recorded from the subantarctic, it is the world's southern-most orchid (Brown et al. 1978). *Nematocerus dienema* has a patchy distribution and grows in wet mire communities. During this study, rabbit diggings and scratchings were observed to be destroying adult plants in several locations. *Galium antarcticum* was found in the 1980s by Rod Seppelt. The record was of a very small plant growing in one location near an upland lake. A specimen was collected and lodged, however subsequent searches have been unable to locate the species.

Cushion plants

Azorella macquariensis and *Colobanthus muscoides* are true cushion-forming species. *A. macquariensis* is most abundant on the high upland plateau however, it can occur at all altitudes with several individuals occurring at sea level, where they are restricted to rockstacks. *A. macquariensis* is regarded as endemic species.

Colobanthus muscoides is predominantly found at sea level, where it is common in the salt-spray zone adhering to rocks and is traversed by penguins and seals. In most situations the species forms cushions in the true sense, tight, compact and spherical however, its habit is more varied than *A. macquariensis*. In southern west coast bays it grows in large continuous mats several hundreds of meters long, and over 1.5 m deep. Referred to by expeditioners as 'the bowling green', this vegetation is extremely susceptible to human trampling.

Plate 1.7 Continuous *Colobanthus muscoides* cushion amongst tall tussock grassland, Precarious Bay September 2000

Prostrate woody shrubs

Some researchers refer to *Coprosma perpusilla* as a prostrate shrub (Jenkin 1972; Lewis-Smith 1984) as it has woody stems, although the species stands no higher than 10 cm. With a patchy distribution across the island, it occurs in mires, wet herbfields and sheltered feldmark communities. *Coprosma perpusilla* is dioecious, having separate male and female plants. The patchy occurrence of one woody species on Macquarie I. highlights a major difference between subantarctic and arctic vegetation which is dominated by several species of prostrate woody shrubs, such as *Salix* sp. and *Betula* sp. (Körner 1999)

Aquatic plants

There is one true aquatic plant, *Myriophyllum triphyllum* which grows in upland freshwater lakes although at times *R. crassipes* can be found growing submerged on the edges of freshwater lakes and streams.

Alien plant species

Many of the species on Macquarie I. occur elsewhere in the subantarctic, or from the surrounding biogeographic regions (ie. New Zealand, Tasmania) and only three species are endemic. Five alien species have been recorded from Macquarie I. (*Anthoxanthum obcordatum, Cerastium fontanum, Poa annua, Rumex crispus, Stellaria media*). Currently only *C. fontanum*, *P. annua* and *S. media* grow on the island (Frenot et al 2004). The most common widespread alien species is *P. annua.* The other two occur as widespread but locally rare interstitial herbs.

Plate 1.8 *Poa annua* with inflorescences

Poa annua was most probably introduced by sealing gangs in the 1800s. Despite having a broad altitudinal range and growing in all habitats, the species does not dominate in any community, other than cobbled beach edges. Abundant in tall tussock grasslands, where it forms thick continuous carpets, *P. annua* thrives on animal derived nutrients (Erskine et al. 1998). *P. annua* is an early coloniser of landslips and rabbit damaged areas, and is positively influenced by human trampling (Scott and Kirkpatrick 1994). The species flowers throughout the year showing it is well adapted to the subantarctic environment. The species has been shown to have high phenoptypic plasticity (Frenot et al. 1999).

Stellaria media and *Cerastium fontanum* subsp. *fontanum* are two small herbs low in stature, and thought to be recent introductions. *C. fontanum* is widespread but rare, whilst *S. media* has a restricted distribution, forming small patches in herbfields and short grasslands and is an earlier coloniser of disturbed areas (Jenkin et al. 1982). A single clump of the herb *Rumex crispus* was found in 1980 (Copson and Leaman

1981) and the grass *Anthoxanthum odoratum*, was also found in two small populations adjacent to a walking track. Both species have subsequently been removed by management authorities (Copson and Whinam 2001)

Interactions - Abiotic influences on vegetation

Origin, Geology and Geomorphology

Macquarie I. is an emergent portion of oceanic crust, referred to as an ophiolite complex. (Williamson 1988). The island is an uplifted part of the eastern margin of the Australian Plate, the junction of this plate and the Pacific plate, and their subsequent movement creates the tectonically active Macquarie ridge (Selkirk et al. 1990a). As a result earthquakes are frequent and intense on the island (Selkirk et al. 1990b).

The island is believed to have reached the surface of the ocean relatively recently (Selkirk et al. 1990a). Uplift rates for the island have been calculated to range from 1.5 mm/yr (Colhoun and Goede 1973a) to 14.5 mm/yr (Selkirk et al. 1983a). Adamson et al (1995; 1996) dated the island's emergence (above sea level) to be between 600, 000 and 700, 000 years ago.

The island's geology is the result of crustal accretion during sea floor spreading, resulting in pillow basalts and basalt flows, volcanoclastic sediments and sediments of marine origin. The major rock types are pillow basalts, minor tabular basalts, paraconglomerates, lithicwackes and reddish mudstones, hyaloclastic, volcanoclastic and talus breccias (Selkirk et al. 1990b; Goscombe and Everard 1998). The most

detailed geological work to date is the map "Geology of Macquarie Island" by Goscombe and Everard (1998).

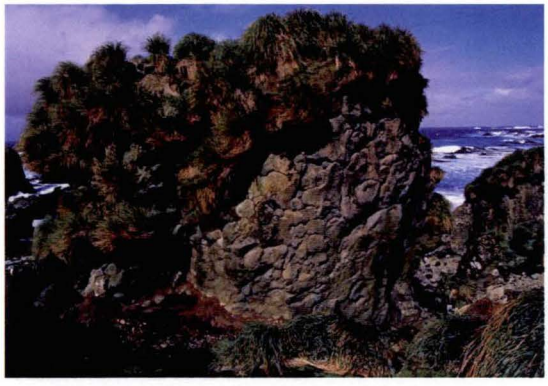


Plate 1.9 Pillow basalts on the coast

Plate 1.10 Serpentinite rocks on the plateau

Rock formations have a significant influence on the vegetation, with no vegetation colonising rocky surfaces such as rock ridges, outcrops, bluffs and scree slopes where loose, particulate rock is too unstable for most plants to colonise. Soils derived from ultramafic rock are generally unfavourable for plant growth. On Macquarie I. areas of serpentine and harzburgite, both ultramafic rock types, support soils which are high in nickel and magnesium. Large areas of serpentine and harzburgite occur on the upland plateau in the northern third the island. These areas have a significantly lower cover of vegetation and more bare ground than on soils derived from the basaltic rock gabbro (Adamson et al. 1993).

The Macquarie I. landscape is strongly influenced by faulting which determines locations of lakes, valleys and creeks. Uplift and faulting have also formed the steep coastal slopes (Selkirk et al. 1990b; Scott 1995). The steepness of these slopes can determine community structure by influencing peat accumulation, hydrology and stability. Plate 1.11 shows the steep coastal slopes of the north west coast, which rise steeply to the plateau.

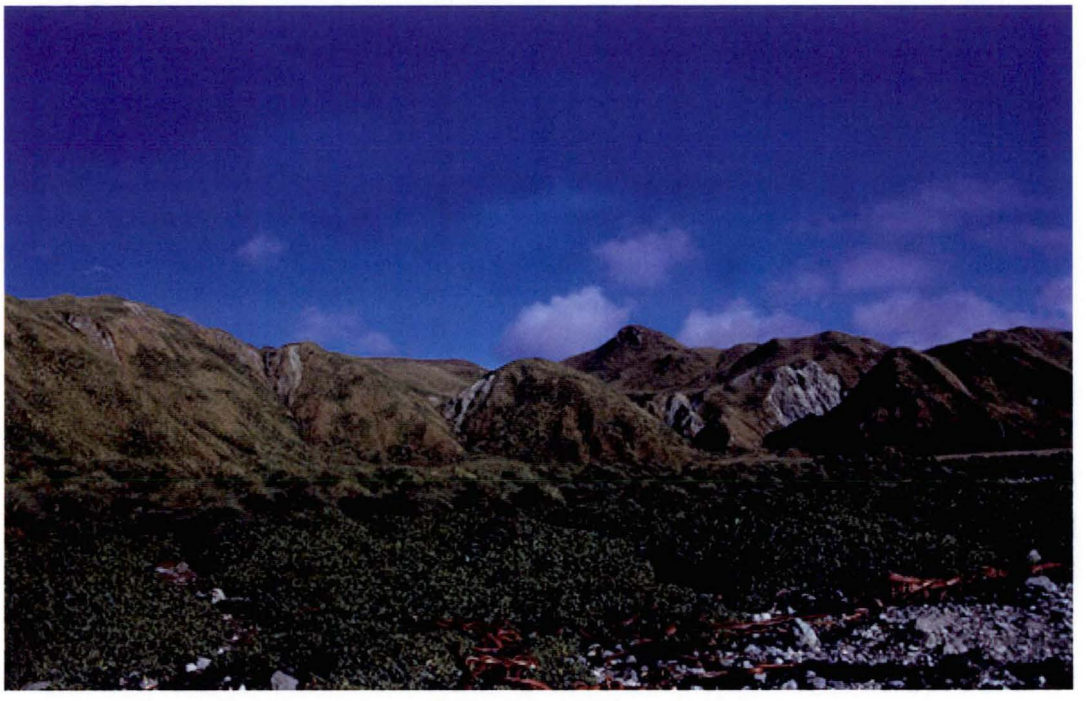


Plate 1.11 Steep coastal slopes dominated by *P. foliosa* and *S. polaris*, with foreground dominated by *Leptinella plumosa.* Half Moon Bay January 2000.

The general shape and topography of the island are visible in Plate 1.12a and b which show the many creeks and lakes, steep coastal slopes and undulating interior.

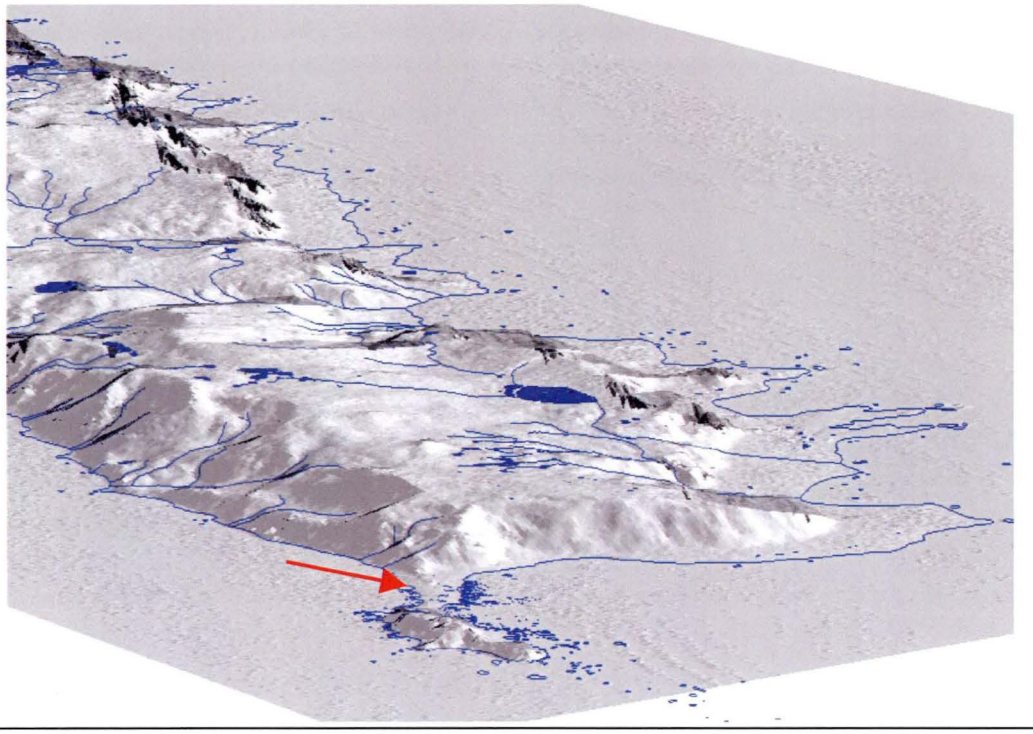


Plate 1.12a. The northern half Macquarie looking south west with the red arrow indicating the isthmus where the research station is situated. The raised marine terrace is visible on the right hand side (western side) of the island. Data courtesy of the Australian Antarctic Data Centre and NASA.

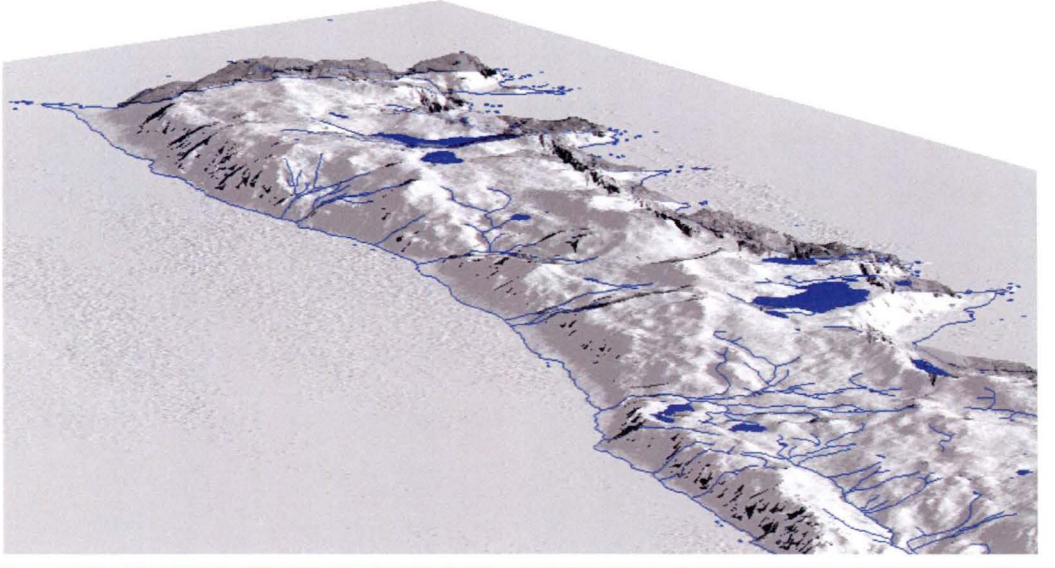


Plate 1.12b. The southern half Macquarie looking south west. The steep coastal slopes of the south east coast are visible, as are the creeks which drain the plateau.

Flat areas with peaty soils become waterlogged and form mire communities, while very steep slopes are too unstable for vegetation. Other geomorphic processes active on Macquarie I, as summarised by Selkirk-Bell (2000), are aeolian, coastal, fluvial, periglacial and mass movement or landslip processes. Aeolian processes are due to the high wind velocities, fluvial are resultant of streams and overland flow, and periglacial processes cause patterned ground. Landslips are common (Taylor 1955; Scott 1983; Scott 1995; Selkirk-Bell 2000) due to the accumulation of deep peats on slopes (5^0 to 35^0) which are then subject to slope overloading with water, windblown mineral material, snow and also tectonic activity which loosens the fabric of the peat (Selkirk 1996). Water is the most important factor influencing slippage of material from slopes, particularly after periods of heavy rainfall (Scott 1985; Selkirk 1996).

Plate 1.13 Landslip after heavy rain in a *P. hookeri* herbfield above Bauer Ck, March 2001.

Plate 1.14 Landslip after heavy rain in *S.polaris/ P. foliosa* tussock grassland along Caroline Creek, December 2000.

As well as increasing the loading of peat, water also acts as a lubricant between the peat and the impenetrable dopplerite layer, which is a humic-iron complex formed beneath the peat (Selkirk 1996). In addition to seismic activity, the denuding of slope vegetation by rabbits is also known to increase the likelihood of landslip. Three major landslips were observed during this study after periods of continuous (24 hours) heavy rainfall events, two of which occurred on slopes which had been subject to heavy rabbit grazing. Figure 1.13 and 1.14 show the exposed peats that form following a landslip. Scott (1995) highlighted an apparent relationship between landslip frequency on coastal slopes and *Stilbocarpa polaris* cover. Landslips appear to be more frequent along the north east coast which is influenced by ongoing faulting processes. *Stilbocarpa polaris* is more abundant on these slopes than on southern slopes which are not derived from the same faulting processes and do not appear to have the same landslip disturbance frequency.

The role of glaciations in shaping Macquarie I. landforms has been much debated over the island's scientific history starting with Blake during 1911-1914 ANARE expeditions (Taylor 1955). Since then there have been numerous opinions on the magnitude of glaciation on the island and its role in the geomorphological history (Colhoun and Goede 1973; Crohn 1986; Goscombe and Everard 1998). During the last glacial maximum, the highest elevation on Macquarie I. was like to be similar to what it is today (Selkirk et al. 1990b). It is quite likely that any glaciation present on Macquarie I. at that time was restricted to small pockets on the upland plateau (Ledingham and Peterson 1984).

Soils

Soil structure varies across the island. The most detailed description of soils to date is by Taylor (1955). Upland plateau soils are usually mineral derived, while lower coastal slopes are rich organic peaty soils. Obviously, the above ground vegetation determines the peat content of soils. Protected, low altitude, high nutrients sites are extremely productive and consequently produce thick, deep peats over 1 m deep. Such soils are common beneath herbfields and tall tussock grasslands. These soils maintain constant temperatures and are often warmer than the ambient air temperature (Tweedie 2000). Fen peats occur on flat or gently sloping ground, supporting mire or herbfields, and can be up to 6 m in depth (Taylor 1955). Mire communities have peats with the water table close to the soil surface, with blanket mires occurring at Green Gorge basin and along the west coast raised beach terraces. In situations where run-off is greatest and terrace is widest and flattest the peats are permanently saturated creating raised mire.

Plate 1.15 *Azorella macquariensis* growing in feldmark mineral soils, west of North Mountain, 350m a.s l.

Mineral soils, common at higher altitudes where organic input is low, are more variable in temperature and have a higher frequency of wind erosion. These soils have lower surface albedo (see Plate 1.15) and insulation and more frequent below ground freeze thaw events than low altitude peatier soils, due to low vegetation cover and lower organic content (Tweedie 2000). Freeze thaw events are more frequent in spring and autumn compared to winter (Tweedie 2000), in periods of drought and high wind these soils were observed to desiccate. No doubt the soil's low nutrient content contributes to the low vegetation cover, consequently erosional processes involving wind water and needle ice are particularly active (Adamson et al. 1993). Beach sand is subject to aeolian processes, in particular constant high speed westerly winds.

Plate 1.16 Mineral beach sand is transported and deposited by wind, as shown here at Bauer Bay, March 2001.

Climate

Climate on Macquarie I. is moderated largely by the surrounding southern ocean and is therefore predominately cool, wet, windy (Selkirk et al. 1990b) and cloudy with frequent precipitation. Macquarie I. has the most equable climate of all the subantarctic islands, with low seasonal differences in air temperature (3.4 °C July and 7 °C January) (Hnatiuk 1975a; Tweedie 2000). Macquarie I. has the lowest annual precipitation of all subantarctic islands (Smith 1993) however, due to constant cloud and fog cover, the island has a low mean daily sunshine hours (2.28 $hday^{-1}$) being higher than only Heard and Campbell Is. (Tweedie 2000). Snow showers are possible on any day of the year, but snow and frost are more common in winter and spring. Climate is the dominant factor affecting vegetation stature and productivity (Jenkin and Ashton 1970). On Macquarie I. the growing season is described as cool, with a long mild winter. Evapotranspiration is highly seasonal being roughly twice as great in summer as in winter (Tweedie 2000).

Altitude has long been recognised as influencing vegetation on Macquarie I. with a reduction in vegetation cover with increasing altitude (Taylor 1955; Jenkin and Ashton 1970; Hnatiuk 1975b; Jenkin and Ashton 1979; Selkirk et al. 1990b; Scott 1995; Misiak unpub; Tweedie 2000) due to associated reductions in air temperature. Several researchers on other subantarctic islands have examined vegetation patterns along altitudinal gradients (Huntley 1971; Walton 1973; Walton 1977a; Lewis-Smith 1984; Smith 1987; Meurk et al. 1994b) finding similar patterns of decreasing vegetation cover, species richness, plant size and reproductive output with increasing altitude.

Aspect determines the exposure and consequently microclimate of a site. The island's strong winds are predominately from the west, therefore slopes with a westerly aspect are exposed to cold, abrasive winds. Southerly weather commonly brings snow, resulting in snow banks forming on south facing slopes. They also receive the least direct sunlight and therefore snow cover persists. The aptly named Windy Ridge is a ridgeline, which runs north-south along the southern end of the island. It falls away gently to the west to an undulating plateau before it reaches the western coastal escarpment. There are no higher peaks to the south of the ridge either and therefore is extremely exposed with strong winds regularly occurring. The presence of mineral soils coupled with regular winds makes Windy Ridge a dry environment at times.

Biotic influences on vegetation

Native invertebrate species

There are 350 invertebrate species, recorded for Macquarie I. of particular note there are 118 Acarina (including parasitic forms), 28 Nematoda, 23 Collembola, 20 native terrestrial Insecta, and five terrestrial Annelida, Mollusca and Araneae (Greenslade in press).

Little is known about the interactions these invertebrates have with vegetation on Macquarie I. Other subantarctic studies have shown that native invertebrates play an important role in nutrient cycling of subantarctic plant communities (Chown and Smith 1993). On Macquarie I. Seven species have distributions which are affected by vegetation, presumably due to microclimatic, food, or an unknown requirement of the animals life history (Davies and Melbourne 1999). *Bradysia watsoni* larvae are

thought to feed on *S. polaris* rhizomes. Aspect was found to be determinate of many species distribution, this may be attributable to a dispersal bias resultant of prevailing wind (Davies and Melbourne 1999).

Native vertebrate species

Millions of marine vertebrates, namely penguins, seals, and sea birds, breed on Macquarie I. during the summer. Tens of thousands of moulting elephant seals (*Mirounga leonina*) deposit faeces, hair, skin and whole carcasses into tall tussock grasslands every year. There are many large colonies of penguins (royal *Eudyptes schlegeli*, king *Aptenodytes patagonicus*, rockhopper *Eudyptes chrysocome*, gentoo *Pygoscelis papua*) on the island, some containing over 500 000 breeding pairs and spanning several kilometers along the coast. Erskine et al. (1998) estimated that 3 730 000 kg of excrement (dry mass) is deposited annually on Macquarie I. by elephant seals royal, king and gentoo penguins. This is likely an underestimate given that colony sizes are now thought to be greater than those used in the original estimations.

On Macquarie I., plants growing near penguin, giant petrel (northern *Macronectes halli* and southern *M. giganteus*), elephant seal, albatross (black-browed *Thalassarche melanophrys*, grey-headed *T. chrysostoma*, light-mantled sooty *Phoebetria palpebrata* and wandering *Diomedea exulans*) and burrowing petrel (several species) colonies or nesting sites obtain nitrogen from these animal sources (Gillham 1961; Erskine et al. 1998) Even plants growing away from animal sources can obtain nitrogen via wind deposition and the volatilisation of ammonia (Erskine et al. 1998). Several species are known to be nitrophilous including *Callitriche antarctica* and *Poa annua. Poa cookii* has a restricted distribution on the island occurring most commonly on the edge or in

the middle of penguin colonies (Selkirk et al. 1990b), or occasionally up slope from nearby penguin colonies, in this nutrient rich situation it most likely has a competitive advantage over the more widely dominant *Poa foliosa*. It has a very strong association with rockhopper penguin colonies, and is most abundant in west coast colonies. Burrowing petrels also influence vegetation through nutrient enrichment (Erskine et al. 1998).

Plate 1.17 Royal penguin colony at Finch Ck, with *P. annua* and *P. foliosa* flourishing at the periphery of the colony.

Vegetation surrounding the colonies is different in colour and often stature to more distant sites. Not only do colonies influence vegetation but some species of burrowing petrel are restricted to specific plant communities (Brothers 1984; Schulz et al. in press). ie. grey petrels (*Procellaria cinerea*) and sooty shearwaters (*Puffinus griseus*) with *Poa foliosa* tussock grasslands, and Antarctic prions (*Pachyptila desolata*) with *Acaena* sp. dominated herbfields. Brothers (1984) stated "prions favoured areas dominated by the dense cover of the buzzy, *Acaena* sp." however, it is possible that

plant species such as *Acaena* sp. may favour burrow activity due to an increase in nutrients, disturbance frequency and seed dispersal. Removal of tussock grasslands by rabbit grazing as observed during this study has caused the disappearance of some burrowing petrel colonies.

Large aggregations of animals cause physical damage to the vegetation. A vegetation complex, dominated by *Poa foliosa* and notably devoid of *Stilbocarpa polaris*, is specific to areas accessible to elephant seals. This is due to the disturbance of animals "between pedestals may considerably hasten erosion of peat, accentuating the height of pedestals" (Selkirk et al. 1990b). When royal and king penguins abandon colonies in winter, large muddy areas devoid of vegetation persist. Southern giant petrels and gentoo penguins have transient colonies which are in a different location each season. It is easy to detect where previous colonies have occurred as the vegetation is altered. Tussocks remain with all small herbs removed and the ground bare. Plate 1.18 shows an area that was previously the site of a southern giant petrel colony where the tussocks have died and small herbs have thrived.

Plate 1.18 *Poa foliosa* tussocks damaged by breeding southern giant petrels, with abundant *Callitriche antarctica* visible, Caroline Point October 2000. (Photograph Aleks Terauds)

Alien species

Alien invertebrate fauna

Greenslade (pers comm.) has identified 25 invertebrate species which are considered synanthropic, meaning they are only found in association with the research station, the main settlement on the northern end on the island. A further 14 species are considered transient aliens, meaning they are not established, and another 14 species are established aliens. The term alien is used here although it is difficult to determine if these organisms have been human-introduced or if they have arrived by their own means. The impacts of these invertebrates on the island's biota are not known.

Alien vertebrate fauna

A complex inter-relationship exists between native and introduced vertebrate species. Several species of vertebrate have been introduced to Macquarie I. since its discovery in the early 1800s. Domestic animals such as horses, donkeys, dogs, goats, sheep, cattle, pigs, ducks and chickens have all been present at some time, usually in close proximity to the station. None of these animals have existed on the island since 1970 (Jenkin et al. 1982). Rats (*Rattus rattus*), mice (*Mus musculus*), cats (*Felis catus*), European rabbits (*Orycolagus cuniculus*) and Wekas (*Gallirallus australis*) were all introduced during the nineteenth century (Jenkin et al. 1982).

Some species, such as rabbits and wekas, were deliberately introduced to supply food for the sealers. Other species, such as rats and mice, were accidentally introduced. The impacts of these animals on the Macquarie I. ecosystem have been the focus of many studies (Costin and Moore 1960; Carrick 1964; Jones 1977; Copson et al. 1981; Jenkin et al. 1982; Selkirk et al. 1983b; Brothers and Skira 1984; Brothers et al. 1985;

Copson 1986; Brothers and Copson 1988; Scott 1988; Pye 1993; Copson and Whinam 1994; Scott 1996; Copson and Whinam 1998; Pye et al. 1999; Pye 2000; Copson and Whinam 2001).

The removal of cats from Macquarie I. has and will continue to have many ecological ramifications. Cats have had a major impact on the island's burrowing bird populations. Since eradication of cats in 2000, several populations of burrowing bird have expanded and some have been found breeding for the first time (Schulz et al. in press.) A flow on effect of this will be an increase in nutrient availability to high altitude areas, as many burrowing birds nest in these upland areas. Changes in vegetation will occur as a result, with Copson and Whinam (2001) predicting an expansion of tussock. However, cats also preyed on rabbits (Jones 1977) and consequently with the reduction in cat numbers, there has been an increase in rabbit numbers.

Rabbits were first introduced to the north east end of the island by sealing gangs in 1879 and by 1894 they had spread to the southwest (Cumpston 1968). By the mid 1960s the population was estimated to be 150 000 (Sobey 1973 in Scott 1988) and then fluctuated over the next decade, again being measured at 150 000 in the mid 1970s (Copson et al. 1981). The damage to vegetation was patchy and varying in intensity, with the large megaherbs and tussock grasses being most affected (Copson and Whinam 1998). In November 1978, the Myxomatosis virus was introduced to Macquarie I. as a means of rabbit population control. This strategy successfully decreased the rabbit population and subsequently the vegetation responded well (Copson and Whinam 1998). However, as a result of a recent succession of dry

winters and the eradication of cats, the rabbit population is again expanding (DPIWE unpub. data) with large tracts of vegetation again being damaged.

The expansion of rabbits has also been aided by the gradual increase in resistance to the myxoma virus of the rabbit population (Copson pers. comm.). Of all the introduced species to impact on the vegetation of Macquarie I. rabbits have had the greatest impact, which at an ecosystem level has been deleterious. Through burrowing activity rabbits increase erosional processes and influence breeding success of burrowing petrels and albatrosses (Warham 1967; Schulz et al. in press.). The degradation and change to vegetation on Macquarie I. due to rabbit activity has been investigated by numerous researchers (Taylor 1955; Costin and Moore 1960; Gillham 1961; Carrick 1964; Ashton and Jenkin 1965; Cumpston 1968; Jenkin and Ashton 1970; Jenkin 1972; Jones 1977; Jenkin and Ashton 1979; Jenkin et al. 1982; Scott 1983; Selkirk et al. 1983b; Brothers 1984; Copson 1984; Scott 1985; Brothers and Copson 1988; Scott 1988; Selkirk et al. 1990b; Frenot and Gloaguen 1994; Scott 1995; Copson and Whinam 1998; Tweedie 2000; Copson and Whinam 2001; Schulz et al. in press.). All studies found that rabbits grazing, digging and burrowing negatively impact the vegetation and the breeding habitat of numerous seabirds on Macquarie I.

This study was not intended to be an investigation into rabbit grazing and its associated impacts, however, it has been impossible to avoid documenting their role in the Macquarie I. ecosystem and consequently various impacts will be discussed through out this thesis.

The aims of this thesis are:

- to summarise current knowledge of reproductive ecology of subantarctic plants
- to identify the prevalence and timing of sexual reproduction in Macquarie Island plant species
- to investigate seed rain and dispersal in Macquarie Island plant species
- to determine and compare biomass allocation in flowering megaherb species
- to quantify seedling emergence and survivorship in megaherb species and to determine the impact of introduced alien species on seedling survival
- to estimate demographic patterns in *Pleurophyllum hookeri*
- to improve our understanding of the importance of sexual reproduction in the subantarctic environment.

Chapter 2 – Reproductive ecology

Reproductive ecology in the Subantarctic

Introduction

The persistence of plant species in a community depends upon mechanisms that enable population growth and sustainability. This chapter investigates the reproductive ecology of vascular plants. There are three main parts to this chapter. The first part is an introduction to the reproductive strategies of plants in the subantarctic environment and provides a summary of previous studies. The second part of this chapter presents an investigation of reproductive ecology of Macquarie I. vascular plants, based on field observations of flowering, seed dispersal and germination of most species. The final component of the chapter investigates seed rain and seed dispersal across nine sites, and discusses the variation in species seed rain between different plant communities.

Sexual reproduction in the subantarctic

Subantarctic plants are extremely productive despite the cool and cloudy climate in which they grow (Costin and Moore 1960; Ashton and Jenkin 1965; Jenkin and Ashton 1970; Hnatiuk 1975a; Lawrence and McClintock 1989; Nicholls and Rapson 1999). In an early study at southern latitudes, Brown (1906) stated 'it is doubtful if a flowering plant could obtain requisite heat needed for its various life functions even to reach the flowering stage, when maturation of its fruits would be impossible' (Brown 1906 in Lewis Smith 1984). Many species of subantarctic plants are near their

physiological limits (Tweedie 2000a) and it might be assumed that most of their resources are utilised in maintenance and vegetative growth. However, despite the challenging climatic environment, subantarctic plants do produce an abundance of flowers, inflorescence, seeds and fruits (Walton 1985). The processes and significance of sexual reproduction in the life cycles of subantarctic plants are little understood despite 100 years of subantarctic botanical research.

Lewis-Smith (1984) suggested that due to the continuation of vegetative growth through winter, seed viability may not be critical in the life cycles of southern latitude plants. However, at an ecosystem level, sexual reproduction is extremely important in the subantarctic, for population recruitment, primary colonization and plant regeneration of areas denuded by natural disturbance, human and introduced vertebrate activity (Scott 1981; Selkirk et al. 1983b; Scott 1988; Frenot and Gloaguen 1994; Scott and Kirkpatrick 1994; Copson and Whinam 1998). At a species level, sexual reproduction facilitates genetic variability and increases chances of dispersal and colonization (Silvertown and Charlesworth 2001).

Many studies have shown that alpine and arctic plants do not rely on sexual reproduction (Billings and Mooney 1968; Billings 1974; Lewis and Callaghan 1976; Bliss 1979; Bell and Bliss 1980; Lewis-Smith 1984; Körner 1999; Costin et al. 2000) Due to climatic similarities, comparisons between subantarctic and arctic plants are commonly drawn (Callaghan and Lewis 1974; Billings 1974; Lewis-Smith 1984; Körner 1999). Clearly such comparisons are not always appropriate given that subantarctic plants allocate large amounts of resources to sexual reproduction (Tallowin and Smith 1977; Jenkin and Ashton 1979; Lawrence and McClintock 1989;

Scott 1995; Tweedie 2000) while Arctic plants largely rely on vegetative reproduction. Convey (1996) investigated reproductive allocation in two vascular plants on subantarctic South Georgia and maritime Antarctica. One species of small pearlwort (*Colobanthus quitensis*) had greater allocation to reproductive biomass in the subantarctic than in the maritime Antarctic environment. Comparatively a grass (*Deschampsia antarctica*) had greater allocation to reproductive biomass in maritime Antarctica than on South Georgia. Apomixis is common in arctic vascular plants yet it has only ever been recorded in the subantarctic for a non-indigenous, alien species (Johnston et al 1993 in Frenot 1999). Some plants are more likely to reproduce sexually in environments where there is a low probability of surviving the next season, while others invest in vegetative biomass to ensure survival and resources can be maintained. Smith and Convey (2002) investigated the sexual reproduction in maritime Antarctic mosses and found that many species could be considered opportunistic short-lived colonists tolerant of unstable and fluctuating conditions able to attain greatest sexual reproductive output near their geographical and physiological range.

There a no simple models that can be applied to plant reproductive performance in the subantarctic. Sexual reproduction consists of several steps starting with floral initiation followed by pollination, seed development and fruit maturation, dispersal, and culminating in successful germination. The following text discusses some of these processes in subantarctic plants.

Flowering & Pollination

Plants experiencing cold summer climates exhibit several reproductive traits for the production of propagules. Billings (1974) summarised these as; preformation of inflorescences, entomophilous (insect pollinated) flowers, abundant anemophilous (wind pollinated) flowers, cleistogamy, self compatibility and self fertilization. Preformation refers to the processes where inflorescences are formed and most cell division completed in the season prior to a flowering event. In some situations preformation begins two seasons prior (Körner 1999). This strategy occurs in subantarctic plants (Lewis-Smith 1984; Walton 1985; Tweedie 2000) however only one study has investigated floral preformation in six vascular species on Macquarie I. (Tweedie 2000) and it was not detected.

In one of the few studies on pollination ecology of subantarctic plants, (Walton 1982) demonstrated that the flora of South Georgia showed two major reproductive strategies; wind pollination and self compatibility. Few alpine and tundra plants are self incompatible (Molau 1993). The ability to self pollinate is a reproductive assurance mechanism under harsh abiotic environmental conditions (Totland & Schulte-Herbruggen 2002) which reduces the dependence of external pollen vectors and may increase reproductive success in environment where few vectors are present. On Macquarie Island, wind is a likely vector of pollination for many species, due to its prevalence and persistence. Approximately a quarter of the island's species are graminoids, which are typically wind pollinated. Wind has also been identified as a common dispersal vector of pollen for plants growing on Campbell I. (McGlone and Meurk 2000).

Bergstrom et al. (1997) found three species of small herb on Macquarie Island to be cleistogamous thus reducing their chances of cross-pollination. The authors also suggested that two other species, *Stilbocarpa polaris* and *Poa annua*, may be self fertilizing. However, Tweedie (2000) identified *S. polaris* as being facultatively xenogamous, and therefore a species which outcrosses ie. the ovules are fertilised by pollen from another flower. It is possible that both processes can occur. Additionally, he identified *Agrostis magellanica*, *L. crinita*, *Acaena magellanica* and *A. minor* to all be facultatively autogamous, meaning fertilisation takes place within the same flower.

Insect pollination is not common on Macquarie Island (Bergstrom et al. 1997) Invertebrate diversity is low with just over 350 invertebrate species, recorded for the island (Greenslade in press). Twenty of these are native terrestrial Insecta, of which Greenslade (in press) doubted any were obligate insect pollinators. Most of these insects are not winged and therefore are unlikely to be effective pollinators (Greenslade pers comm.).

During the current study, small flies (Diptera) were observed on *Stilbocarpa polaris* inflorescences and their presence coincided with that of pollen laden anthers. These small flies have previously been seen on *S. polaris* (Davies and Melbourne 1999). Small flies have also been seen feeding on the flowers of *Leptinella plumosa* (Greenslade in press). Tweedie (2000) observed kelp flies on *S. polaris* inflorescences during his study on Macquarie I. Greenslade (in press) stated that it is unlikely that any of the flowering plant species are dependent on insect pollination as the Insecta are low in abundance.

Plate 2.1 Flies on *S. polaris* inflorescence, bottom right red arrow points to a fly which is entering the flower (corolla tube)

Walton (1985) characterised insect pollinated flowers in the subantarctic as being small white or yellow flowers. Interestingly, even though there is little evidence of insect pollination on Macquarie I. 85% of the flowering dicots fit this description.

Only two plant species on Macquarie Island are dioecious; *Poa foliosa* (Edgar 1986; Tweedie 2000) and *Coprosma perpusilla* (Taylor 1955; Lloyd and Horning 1979), with the remainder being monoecious (Hnatiuk 1993) (see Plate 2.2a and 2.2b). In a study on modern pollen rain on Campbell I. (McGlone and Meurk 2000) *Coprosma perpusilla* was found to disperse abundant pollen detected well away from parent plants. Undoubtedly this enables successful reproduction in this dioecious species without the need for female and male plants to occur in close proximity.

Plate 2.2 a Female *Coprosma perpusilla* flowers with stigma visible

Plate 2.2 b Male *Coprosma perpusilla* flowers with anthers visible

At a community level pollination appears to be successful given the vast amount of seeds and seedlings observed during this study. However further studies are needed to investigate pollen limitation on seed set, seed viability, self compatibility for all

species. Genetic studies may reveal whether there is temporal separation in pollen release and stigma receptivity for various species.

Further studies are needed to investigate the occurrence of apomixis and polyploidy in Macquarie I. plant species. Chromosome numbers of arctic plants were found to vary across different environments (Murray and Kelso 1997). *Poa annua*, the most common alien in the subantarctic, displays polyploidy (Frenot et al. 1999) and apomixis has also been observed in this species ("Johnson et al 1993" in Frenot et al. 1999).This reproductive plasticity may explain its globally widespread colonising capacity. *Poa litorosa* growing in New Zealand was found to exhibit a very high level of polyploidy (Edgar 1986). The chromosome number of *P. litorosa* in the Macquarie I. population has not been recorded.

Long distance seed dispersal

The low species diversity on Macquarie Island is largely attributable to low mean temperature and isolation (Greve et al. 2005). As the island is an ophiolite complex, colonisation of the island by plants has occurred through long distance dispersal over time. With only three endemic species on Macquarie I. all other species have wider distributions. Twelve species occur in New Zealand and on the New Zealand cool temperate Is, three species occur in southern Australia, 14 species have a southern hemisphere distribution while one species (*Montia fontana*) also occurs in the northern hemisphere. The broad distribution of these species across the southern ocean and southern hemispheres, where land bridges are few, is evidence of long distance dispersal.

Long distance dispersal via "wind highways" explains floristic similarities in cryptogams and ferns of subantarctic islands (Munoz et al. 2004) and this may also be true for small seeded plants. Seabirds are the most likely vector for large fruits and seeds and thousands visit the island throughout the year. *Acaena* spp. and *Uncinia* spp. on Macquarie I. have hooked fruits. Several species of albatrosses, northern and southern giant petrels and subantarctic skua have been observed with *Acaena magellanica* and *Acaena minor* fruits adhering to their feathers. Most species do not have obvious attachments however, Taylor (1954) described *S. polaris* fruits adhering to the feet of a black–browed albatross with regurgitate oil. Unusually strong winds are considered to be likely vectors of dispersal for occurrences of previously unrecorded insects on Macquarie I., it is possible that such winds could also transport seeds.

Poa litorosa and *Carex trifida* are rare species on Macquarie I. They are common on the Antipodes Is., the Snares, and Campbell I. Both species grow on a raised coastal terrace at Handspike Point in the NW of Macquarie I. *P. litorosa* also occurs in an isolated pocket at Caroline Cove in the SW of the island. It is not known what restricts the distribution of both species. It may due to rabbit grazing, loss of a local disperser, or they may simply be recent introductions. The two locations where *P. litorosa* occurs are approximately 30 km apart and quite different habitats. One is a low altitude, waterlogged mire and the other is a steep, mid-altitude, short grassland. Wandering albatross (*Diomedea exulans*) breed at both sites and it is possible they may have acted as a vector between these isolated sites or have been responsible to for separate introductions. A close congener of the wandering albatross, the antipodean albatross, *Diomedea antipodensis,* endemic to the Antipodes Is. has been

observed at Caroline Cove (pers. comm. Aleks Terauds) and therefore this species is also a potential vector of seed dispersal. Skuas and kelp gulls may also be vectors of dispersal, interestingly though these birds are widespread across the island while *Poa litorosa* has a restricted distribution (ie. it has not dispersed from the two sites) similar to that of the wandering albatrosses on the island. The distribution of *Carex trifida* on Campbell I. is strongly related to the presence of nesting seabirds (Meurk et al. 1994b).

Plate 2.3 *Poa litorosa* growing on a raised marine terrace at the north west of the island, Handspike Corner, January 2001.

There is no conclusive evidence to suggest that these birds have acted as a dispersal vector introducing *P. litorosa* from the Antipode Is. However, it is possible to see how such processes could occur on oceanic islands. Huntley (1971) found that high densities of wandering albatross (*D. exulans*) nests on Marion Island led to the replacement of original vegetation by a distinctive grass and forb community. Dean et al. (1994) investigated plant colonisation of yellow-nosed (*Thalassarche cholorhynchos*) and sooty albatross (*Phoebetria fusca*) nests in South Atlantic Ocean islands. The study showed that cleared ground around albatross nests provides habitat for indigenous and alien plant seedling establishment. The ratio of alien to indigenous plants altered and the number of indigenous species significantly increased with time after nest desertion. On Macquarie I. prior to human arrival, the number of wandering albatross nesting on the NW raised coastal terrace was potentially 30 times greater than at present (Gillham 1967).

No doubt long distance seed dispersal could also be facilitated by other vagrant bird species which visit the island. During this study, cattle egrets, pigeons, sooty albatrosses (*Phoebetria fusca*), snow petrels (*Pagodroma nivea*) and ruddy turnstones were observed on Macquarie I. Other bird species such as songthrush (*Turdus philomelus*) and blackbirds (*Turdus merula*) have been often observed, as well as seed eaters such as yellowhammer (*Emberzia citronella*) and chaffinch (*Frigilla coelebs*) (Martin Schulz pers comm.). Many vagrant birds have been seen at Handspike Point, perhaps because it is the largest, flattest, and most northern, coastal area on the island and it is close to the research station. Despite the presence of all these birds in the vicinity of the plant it is interesting that it has not spread further on the island, which suggests that either dispersal by birds across the island is not effective or germination

requirements are not met, or perhaps it is due to rabbit grazing patterns. These issues are further discussed in Bergstrom and Turner et al (in press).

Barber et al. (1959) discussed the likelihood of seeds being transported to the island by driftwood originating from Tierra del Fuego that reached Macquarie I. Several plant species are common between the two regions (ie. *Callitriche antarctica, Blechnum penna marina, Acaena magellanica).* More recently, the discovery of an individual plant of *Leptinella plumosa* (Asteraceae) on subantarctic Heard Island appears to be evidence of long distance dispersal (Turner et al. 2005). The plant was found in an area where vegetation appears to be expanding. It has a sticky seed coat (Taylor 1955; Bergstrom 1986a; Webb and Simpson 2001) and on Marion I. was affiliated with wandering albatross nests (Huntley 1971). Deglaciation has continued to occur on Heard I. long after the last glacial maximum, resulting in new areas of land appearing at low altitudes. The recent discovery of this new species indicates that establishment may be governed more by niche availability than dispersal.

Plant species have also been introduced across the subantarctic via human-mediated dispersal (Walton and Smith 1973; Copson and Leaman 1981; Jenkin et al. 1982; Bergstrom and Smith 1990; Frenot and Gloaguen 1994; Lewis-Smith 1996; Chown et al. 1998b; Frenot et al. 2005; Whinam et al. 2005). A recent phenomenon in the subantarctic (arriving within the last 200 years), these introduced (or alien) plants are displacing and disrupting natural plant communities on several islands (Gremmen 1981; Gremmen 1997; Gremmen et al. 1998; Frenot et al. 2001). This presents a large array of problems to island land managers. On Macquarie I. two species (*Rumex crispus* and *Anthoxanthum orbcordatum*) have been introduced and subsequently

eradicated. Three other species (*Poa annua*, *Stellaria parviflora*, and *Cerastium fontanum*) are now well established and successfully sexually reproducing. Fortunately they do not appear to have displaced any native species and to date appear to have had no deleterious impacts on the island's plant communities (Brothers and Copson 1988). This is most likely due to the species' attributes as other alien plant species on other subantarctic islands have displaced indigenous species (Frenot et al. 2005).

Small scale seed dispersal

Little is known of small scale or intra-island dispersal processes. The occurrence of isolated individual plants on cliff faces and in the middle of unvegetated rocky screes, indicates that successful dispersal occurs within the island. Scott (1995) found that the colonisation of landslips occurs through both vegetative fragments and seed germination. Dispersal vectors within the island are most likely gravity, wind, snow melt, water, seabirds and introduced vertebrates, particularly rabbits and possibly land birds such as Red Polls. Small grass seeds and the plumose achenes of *Pleurophyllum hookeri* can be seen blowing in the wind. Wind-blown, ripe inflorescences of *S. polaris* have been observed rolling across the island's upland plateau, in a tumbleweed-like fashion. It is likely that the inflorescences originated from *S. polaris* plants on the coastal slopes and as *S. polaris* was absent from the area where inflorescences were seen.

Throughout the year snow banks form in many areas, particularly on the island's upland plateau. When the snow melts, small piles of detritus are deposited. These piles contain plant fragments and seeds, which have been abraded from the vegetation

by the action of accumulating and melting snow. Once the snow melts, run-off transports these seeds.

A similar action occurs after heavy rain, when flowing water transports seeds. Such processes are examples of secondary dispersal, where seed is further dispersed following deposition from the inflorescence. The introduction of alien vertebrate species to Macquarie I. has had numerous deleterious effects on the island's ecology (Carrick 1964; Jones 1977; Copson and Leaman 1981; Selkirk et al. 1983b; Brothers and Skira 1984; Copson 1986; Mabberley 1986; Brothers and Copson 1988; Copson and Whinam 1994; Scott 1995; Copson and Whinam 1998). As well as causing mechanical damage, rabbits also act as dispersal vectors. The spined achenes of *A. magellanica* and *A. minor* are commonly found on rabbit carcasses and *Acaena* spp. dominate in areas with dense rabbit burrows, indicating that rabbits are likely to be an important factor in the distribution of *Acaena* spp.

Plate 2.4 Tasmanian Parks and Wildlife cat hunting dog 'Kim' indicates how *Acaena magellanica* and *Acaena minor* fruits adhere to fur. There are no native terrestrial furred animals on Macquarie I.

There are no extant terrestrial birds on Macquarie I. (Selkirk et al. 1990b). Ground parrots (*Cyanoramphus novaezelandiae*) and land rails were present prior to the arrivals of sealing gangs. Sealers regularly ate ground parrots and as did introduced dogs and cats (Cumpston 1968), all of which decimated the population. As they were gramnivorous, it is likely that these birds assisted in dispersal (Taylor 1979). A closely related subspecies of the ground parrot on neighboring NZ subantarctic islands are generalist feeders, commonly foraging on *Carex trifida* seeds (Taylor 1985). The human-induced disappearance of these dispersal vectors may help explain the restricted distribution of *C. trifida* on Macquarie I. however, little is known of its distribution pre-human arrival.

The introduced red poll has been observed by several researchers feeding on *P. hookeri* seeds (Jenkin et al. 1982). During this study, it was also observed feeding on *L. plumosa.* It is not known if seeds would survive the gut of this species however it bears consideration that red polls may now act as a dispersal agent for these species and others. Small scale dispersal processes are further discussed later in this chapter.

Soil seed banks

A study of soil seed banks of major communities on Macquarie I. found extensive seed banks existed at all sites ranging from 667 seeds m^{-2} to 96 333 seeds m^{-2} (Misiak unpub. data). Seed banks floristic composition reflected that of the standing vegetation. The size of the soil seed bank could not be correlated with change in altitude and corresponding temperature change.

This was the first study of its kind in the subantarctic. The seed densities found far exceeded those reported for alpine and arctic areas, highlighting that sexual reproductive outputs of some taxa are high and widespread (Misiak unpub.). However, there are obvious limitations in using seed banks as indicators of standing vegetation performance. The viability, origin and age of the seeds are not known. Quantification and timing of reproductive output of nearby standing species can not be determined by seed banks alone.

Seed germination

For germination to occur seeds must be healthy, with a viable embryo. Many environmental factors influence seed health prior to dispersal, particularly during the developmental and ripening phases. For plants growing at their environmental limits resources available for fruit and seed production may be limited but very few studies have assessed viability (Dorne 1977; Frenot and Gloaguen 1994; Bergstrom et al. 1997; Hennion and Walton 1997a). Dorne (1977) found that failure to germinate in several subantarctic species was attributable to physiologically immature seed embryos. He suggested that the endemic species produced large numbers of viable seeds, while widely distributed subantarctic species have low seed viability. Hennion and Walton (1997a) found variation between populations, suggesting a genetic influence on viability. However, determining viability through *ex situ* germination experiments can produce inconclusive results as it is difficult to assess if species germination requirements have been met.

Once healthy, viable seeds are dispersed to an appropriate microsite germination is required to create a functioning plant. Microsite suitability is complex within the

subantarctic environment. There is a trade-off between protection and exposure, with protection contributing to competition from other plants, while exposure results in extremely harsh growth conditions (Walton 1977a).

Seeds may have to lie dormant during winter until spring or summer brings more suitable conditions. Seed longevity depends on seed moisture and lipid content (Lewis-Smith 1984; Baskin and Baskin 1998). Germination requirements are varied amongst species with some requiring vernalization, diurnal fluctuation of temperature, minimum degree hours or a specific substrate (Dorne 1977; Walton 1977b; Lewis-Smith 1984; Hennion and Walton 1997a; Baskin and Baskin 1998) Generally, high temperatures are required to trigger germination in subantarctic species (similar to arctic and alpine species), this temperature requirement would mean that emergent seedlings are not exposed to low winter temperatures (Billings and Mooney 1968; Bliss 1988; Frenot and Gloaguen 1994; Baskin and Baskin 1998; Körner 1999).

In general there are many factors which influence the success of plant propagule dispersal and germination. In the subantarctic, there are added environmental pressures that influence these processes, for example; freeze-thawing of soil, sporadic snow cover, constant low temperatures Several studies question the significance of sexual reproduction in high latitude plants (Billings and Mooney 1968; Bliss 1971; Billings 1974; Lewis and Callaghan 1976; Bliss 1979; Bell and Bliss 1980; Körner 1999), despite the fact that subantarctic plants produce large amounts of seed. Very few researchers have investigated the extent of sexual reproduction in subantarctic vegetation.

Bergstrom et al.(1997) and Tweedie (2000) have investigated reproductive processes of several species (see Table 2.1); however, the most comprehensive study of reproductive processes of all Macquarie I. species is Taylor (1955) (see Table 2.2 and 2.3). By determining the reproductive traits across all life forms of vascular plant species on the island, the role of environmental selection can begin to be investigated.

Table 2.1. Reproductive studies on vascular plants in the subantarctic to date.

Island	Year	Author	Major Spp. studied	Observation
Kerguelen	1977	Dorne	*Acaena ascendens* *Pringlea antiscorbutica* *Azorella selago* *Poa cookii* *Cotula plumosa* *Tillea moschata* *Ranunculus biternatus*	Germination Floral phenology
Kerguelen	1994	Frenot & Gloaguen	*Colobanthus kerguelensis* *Cerastium fontanum* *Azorella selago* *Agrostis magellanica* *Poa annua* *Festuca contracta* *Poa kerguelensis*	Reproductive output Seed viability Seed germination
Kerguelen	1997	Hennion & Walton	*P. antiscorbutica* *P. cookii* *P. kerguelensis* *C. kerguelensis* *Lyallia kerguelensis* *Ranunculus moseleyii* *R. biternatus* *R. pseudotrullifolius*	Germination
Kerguelen	2000	Chapius, Hennion et al	*P. antiscorbutica*	Reproductive traits
Marion	1970	Huntley	*A. selago*	Reproductive ecology
South Georgia	1971	Callaghan & Lewis	*Phleum alpinum*	Reproductive performance
South Georgia	1971, 1977a, 1977b	Tallowin	*F. contracta*	Reproductive biology Floral phenology Reproductive performance
South Georgia	1974, 1977	Callaghan	*P.alpinum*	Reproductive biology
South Georgia	1977	Tallowin & Smith	*F.contracta*	Reproductive biology

Island	Year	Author	Major Spp. studied	Observation
South Georgia	1977, 1979, 1982	Walton	*Acaena spp.* *Calltitrche antarctica* *Colobanthus quitensis* *Colobanthus subulatus* *Deschampsia antarctica* *F. contracta* *Galium antarcticum* *Juncus scheuchzeriodes* *Juncus inconspicuous* *M .fontana* *P. alpinum* *Poa flabellata* *R. biternatus* *Rostokovia magellanica* *Uncinia meridensis* *P .annua* *Poa pratensis* *Taraxacum officinale*	Seed germination Floral phenology Hybridization
Macquarie	1955	Taylor	*All species* (to this date)	General reproductive biology
Macquarie	1979	Lloyd & Horning	*Coprosma perpusilla*	Sex distribution
Macquarie	1986	Bergstrom	Numerous species	Seed atlas
Macquarie	1990	Scott	*Stilbocarpa polaris*	Flowering
Macquarie	1997	Bergstrom et al	*Cardamine corymbosa* *P. annua* *M. fontana* *A. magellanica* *Epilobium pedunculare* *Luzula crinita* *Poa foliosa* *Azorella macquariensis* *S .polaris*	Reproductive behaviour Seed germination Floral phenology
Macquarie	1998	Misiak	All spp.	Seed rain
Macquarie	2000	Tweedie	*L. crinita* *S. polaris* *P. foliosa* *Acaena magellanica* *Acaena minor* *Agrostis magellanica*	Floral phenology Seed germination

Table 2.2 Autecological notes on phenology and floral biology of dicotyledonous species Flora on Macquarie Island. Summary of Taylor (1955)

Species	**Synonymies**	**Flowers**	**Ripe Fruits/seeds**	**Vegetative spread**	**Seed dispersal vector**	**Other info**
Ranunculus crassipes	*Ranunculus biternatus*	Oct-Mar	Dec-Sept	rhizomes	Wind water	Germ by seed
Cardamine corymbosa		Oct- Apr	Nov-June	rhizomes	Wind	Germ by seed
Stellaria parviflora	*Stellaria decipiens-parviflora*	Sept-Apr	Oct- June	Creeping stems	wind	Germ by seed
Stellaria media		Sept-June	Year round	Creeping stems	wind	Germ by seed
Cerastium fontanum	*Cerastium triviale*	Oct- July	Year round		wind	Germ by seed
Colobanthus muscoides		Sept-Mar	Oct- May	Lateral growth of cushion	wind	Germ by seed
Colobanthus affinus Colobanthus apetalus	*Colobanthus crassifolius*	July- Mar	Sept-May		wind	Germ by seed
Montia fontana		Nov-Apr	Dec-May		explosion	Germ by seed
Acaena magellanica	*Acaena ascendens*	Sept-Feb	Nov-May	Creeping stems	animals	Germ by seed
Acaena minor	*Acaena anserifolia*	Sept-Jan	Jan-Apr		animals	
Crassula moschata		March	Apr		wind	
Myriophyllum triphyllum	*Myriophyllum elatinoides*			Hibernacaula		
Callitriche antarctica		Sept-Mar				
Epilboium pedunculare	*Epilobium linnaeiodes*	Oct-Apr	Nov-June		Wind poss.. animals	
Epilobium brunnescens	*Epilobium nerterioides*				Similar to *E. linnaeiodes*	
Hydrocotyle novae-zeelandae	*Hydrocotyle*	Dec-Mar	Feb-June		Feb-June	
Azorella macquariensis	*Azorella selago*	Dec-Feb	Jan-Apr			
Stilbocarpa polaris		Nov-Apr	Jan-Aug		Gravity or water poss. parakeet	
Coprosma perpusilla subsp. subantarctica	*Coprosma pumila*	Dec-Apr	Shed yr round		Rolling poss. weak or parakeet	
Pleurophyllum hookeri		Set-Dec	Dec-Mar			Germ by seeds only
Leptinella plumosa	*Cotula plumosa*	Nov-Mar	Feb-Mar	Creeping		Germ by seed

Table 2.3 Autecological notes on phenology and floral biology of monocotyledonous species on Macquarie Island. Summary of Taylor (1955)

Monocot Species	**Synonymies**	**Flowers**	**Ripe Fruits/seeds**	**Vegetative spread**	**Seed dispersal vector**	**Other info**
Juncus scheucherizoides		Dec-Apr	Feb-July			
Luzula crinita	*Luzula campestris*	Oct-Jan	Jan-Oct (poss. Jan-Jan)		Wind	Germ by seed
Isolepis aucklandicus	*Scirpus auklandicus*	Dec-Feb	March-Sept			Repro. by seeds
Uncinia hookeri	*Uncinia riparia var. hookeri*	Nov-Dec	Jan-Apr		poss. birds	
Carex trifida		Nov-Jan	Apr-Jul			Repro. by seeds
Agrostis magellanica		Nov-Mar	Mar-Dec			
Deschampsia chapmani		Dec-Mar	Mar-May		poss. rabbit fur	
Deschampsia caespitosa	*Deschampsia penicillata*	Feb (once at one location)				
Puccinellia macquariensis		Nov-June	Jan-Jan			
Poa foliosa		Oct-Jan	Feb-May		Wind	
Poa cookii	*Poa hamiltoni*	Nov-Feb	May-Sept			
Poa annua		Sept-June				
Festuca contracta	*Festuca erecta*	Oct-Jan	Dispersed Feb-Oct			

Reproductive ecology on Macquarie I.

This study aimed:

- To identify how prevalent sexual reproduction was in subantarctic plant species.
- To identify seasonality in flowering, seed dispersal and germination.
- To identify any variation in reproductive traits across plant functional groups.

Materials and Methods

The reproductive stages of all flowering species on Macquarie I. were monitored across the island from November 1999 to March 2001, with the exception of *Galium antarctica* and *Deschampsia caespitosa*. *G. antarctica* is known from one site (R. Seppelt pers. comm.) and during this study, after extensive searching, it was unable to be located and *D. caespitosa* has an extremely restricted distribution. The data were

Plate 2.5 *Poa foliosa* inflorescence (female)

collected opportunistically, across a range of altitudes, community types and water and nutrient regimes over the island. This study presents numerous species specific observations at the island scale.

Flowers and fruit were easily detectable through field observations upon close inspection of all species, as shown in Plate 2.1, 2.2 and 2.3. Seedling data are based on general field observations and seedlings that were recorded in seedling plots associated with another study (see Chapter 5). Species identification of seedlings, particularly monocots, is very difficult and usually requires the plant to grow beyond the cotyledon stage, bearing adult leaves, which takes many months and sometimes years. The seedling emergence data presented for each species indicates situations where the seedling morphology is distinctive (i.e. *Cardamine corymbosa*) or where the seed source, an adjacent adult plant, was present with no other related taxa nearby (>50 cm). For example, where there were emergent monocot seedlings amongst *P. foliosa* tussocks and no other monocots were present, the seedlings were presumed to be *P. foliosa.*

Dispersal dates shown incorporate field observations where fresh seed was first observed on the ground or where seed capsules were first observed empty. This data was supplemented with seed rain data from seed traps (see the next section of this chapter – Seed rain on Macquarie I.). For some species no observations were made of a particular stage in the reproductive cycle, this in no way indicates an absence of this stage from the cycle, it merely reflects the opportunistic nature in which the data was collected.

Plate 2.6 Ripe fruits of *Coprosma perpusilla*. Fruits such as this, ie. big, red, and embedded in plant mat are from the previous summer i.e.> 12 months old

Plate 2.7 *Acaena minor* fruits beginning to form on two inflorescences while the third has only dehisced stamens. Note the spiked fruits.

Results & Discussion

A total of 26 species were seen flowering, 22 dispersing and 12 emerging. This represents 72%, 61% and 33 % of the angiosperm flora of the island, respectively. Table 2.4 shows the observations of reproductive performance. Flowering data are the most comprehensive as it was the easiest to detect by observations, with seedling emergence the most cryptic. An attempt was made to record the time at which seeds began to ripen but this became too subjective, therefore dispersal times were obtained, as these indicate when seeds enter the system as individual propagules.

There was a general seasonal trend of flowering in late spring with seedlings emerging in summer, and seed dispersal in late autumn for most species (Table 2.4). The overlap of flowering and dispersal for some species such as *Acaena spp., L. crinita, Agrostis magellanica, F. contracta, U .hookeri*, and *P. macquariensis* is attributable to the persistence of seeds on parent plants even after the fruit has ripened. *Coprosma perpusilla* was observed retaining its fruits from the previous season whilst the new season's fruit were ripening (Plate 2.6). No dispersal was observed for this species which bears red fleshy fruits, and therefore is thought to be suitable for bird dispersal. *Nematocerus dienema* (the rare orchid) displayed deciduousness with adult leaves disappearing during winter and then re-emerging in spring, with some individuals not flowering in consecutive years.

Other subantarctic studies (Gremmen 1982; Tweedie 2000) have found that flowering phenology varies with altitude, with coastal sites commencing flowering prior to high altitude sites. This trend was apparent in general field observations but not quantified,

all species observations were made across a range of altitudes wherever possible, as some species are restricted in distribution. This study presents general seasonal trends for each species where possible, but it is acknowledged that phenologies do vary with altitude. *Poa annua* was the only species that flowered throughout the year with all other species displaying seasonal flowering patterns. Five out of 36 species commenced flowering in September and another seven were flowering by October. Most species flowered for only three to four months, however, the megaherb species flowered for approximately six months although this was partially due to a variation in flowering time with altitude.

Poa foliosa was the first species to commence dispersal, with seeds being shed as early as January, while four other species began in February. By March, 30% of all species monitored were dispersing suggesting that these species only take a few months for seeds to ripen. *Stilbocarpa polaris* and *Uncinia hookeri* were the only winter dispersing species observed. *Luzula crinita, Acaena spp.* and several of the grass species retained fruit on the adult plant long after they had ripened, however *L. crinita* was the only species observed to display vivipary.

Although only a preliminary, opportunistic study, these observations do indicate that there is a strong seasonality to flowering phenology, with all except one species flowering and fruiting in spring and summer. As a group, small herbs had the shortest period of flowering (3-5 months). Despite the island's equable climate (Hnatiuk 1975a; Tweedie 2000) sexual reproduction was seasonal coinciding with an increase in daylength and for many plants an expansion in vegetative growth. The data also show that 72 % of angiosperms present on Macquarie Island were observed flowering

and producing seeds, indicating that sexual reproduction is indeed ecologically important in this habitat.

Table 2.4. General observations of reproductive cycle of flowering plants, indicating flowering (red), seed dispersal (grey), and seedling emergence events (green).

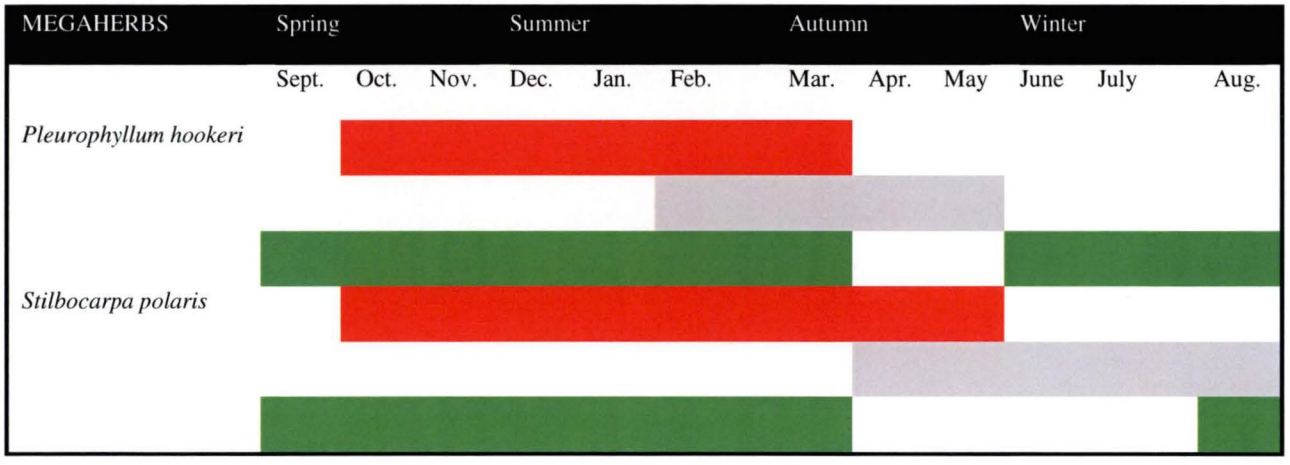


Table 2.4. (cont) General observations of reproductive cycle of flowering plants, indicating flowering(red), seed dispersal (grey), and seedling emergence events (green).

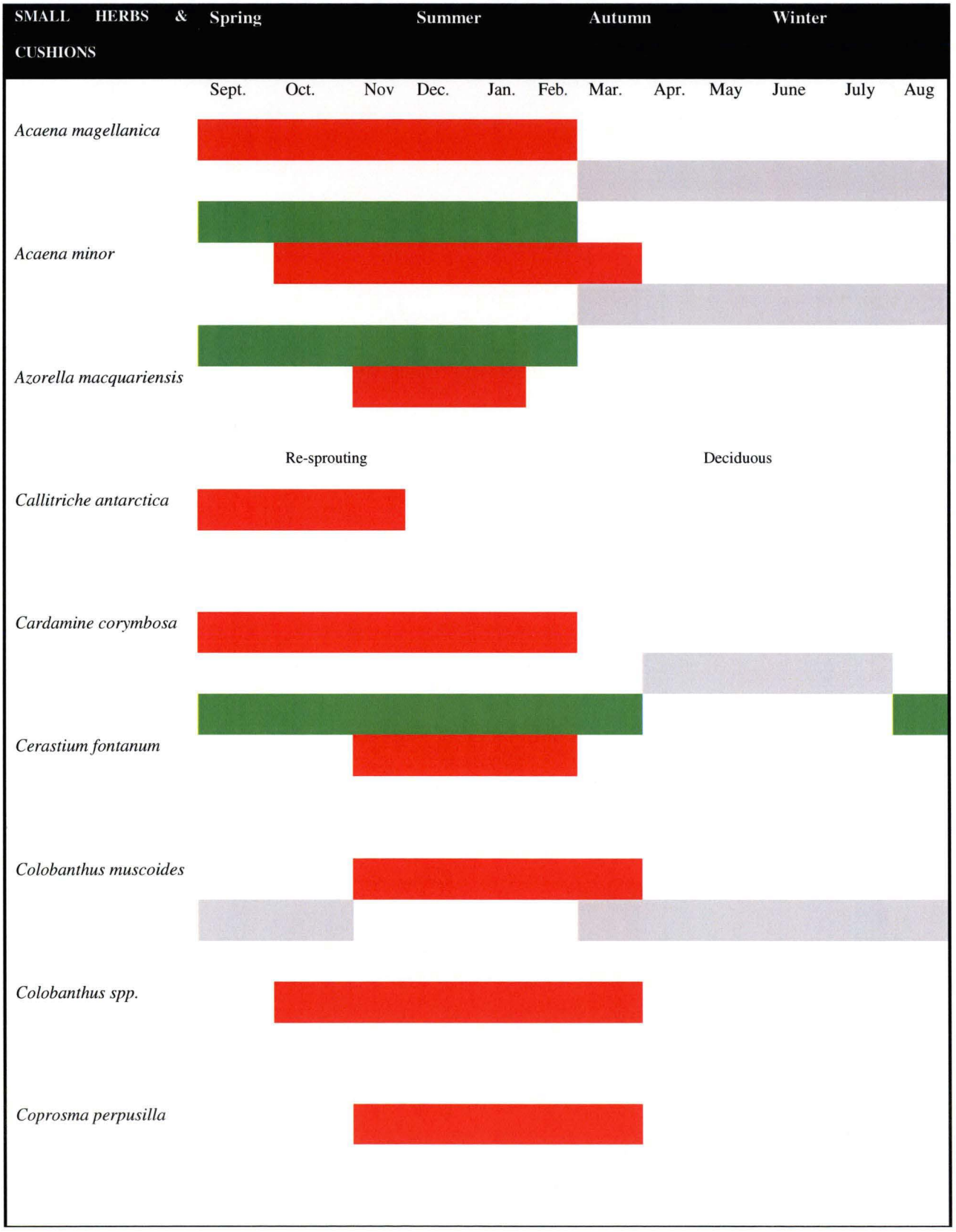


Table 2.4. (cont) General observations of reproductive cycle of flowering plants, indicating flowering(red), seed dispersal (grey), and seedling emergence events (green).

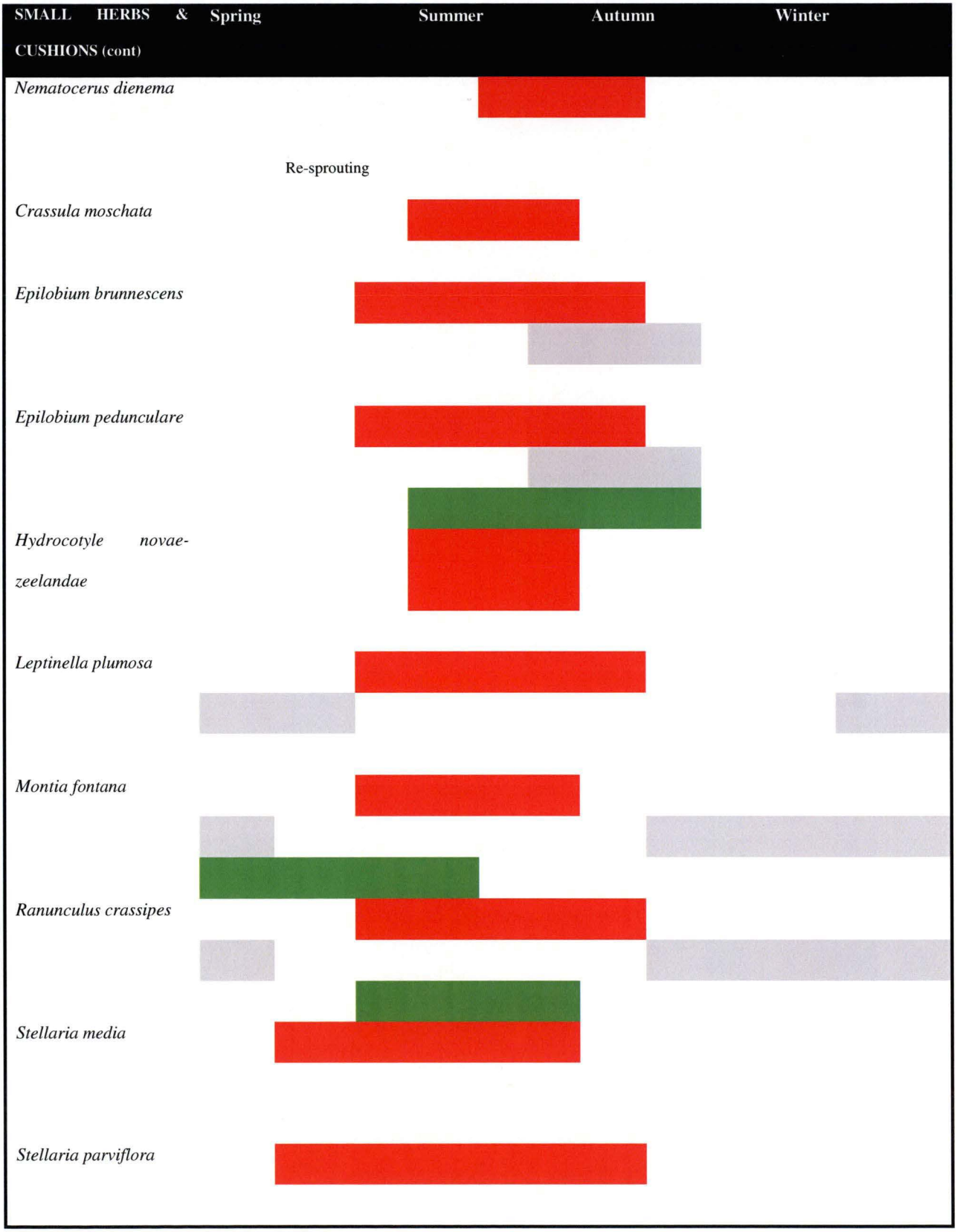


Table 2.4. (cont) General observations of reproductive cycle of flowering plants, indicating flowering(red), seed dispersal (grey), and seedling emergence events (green).

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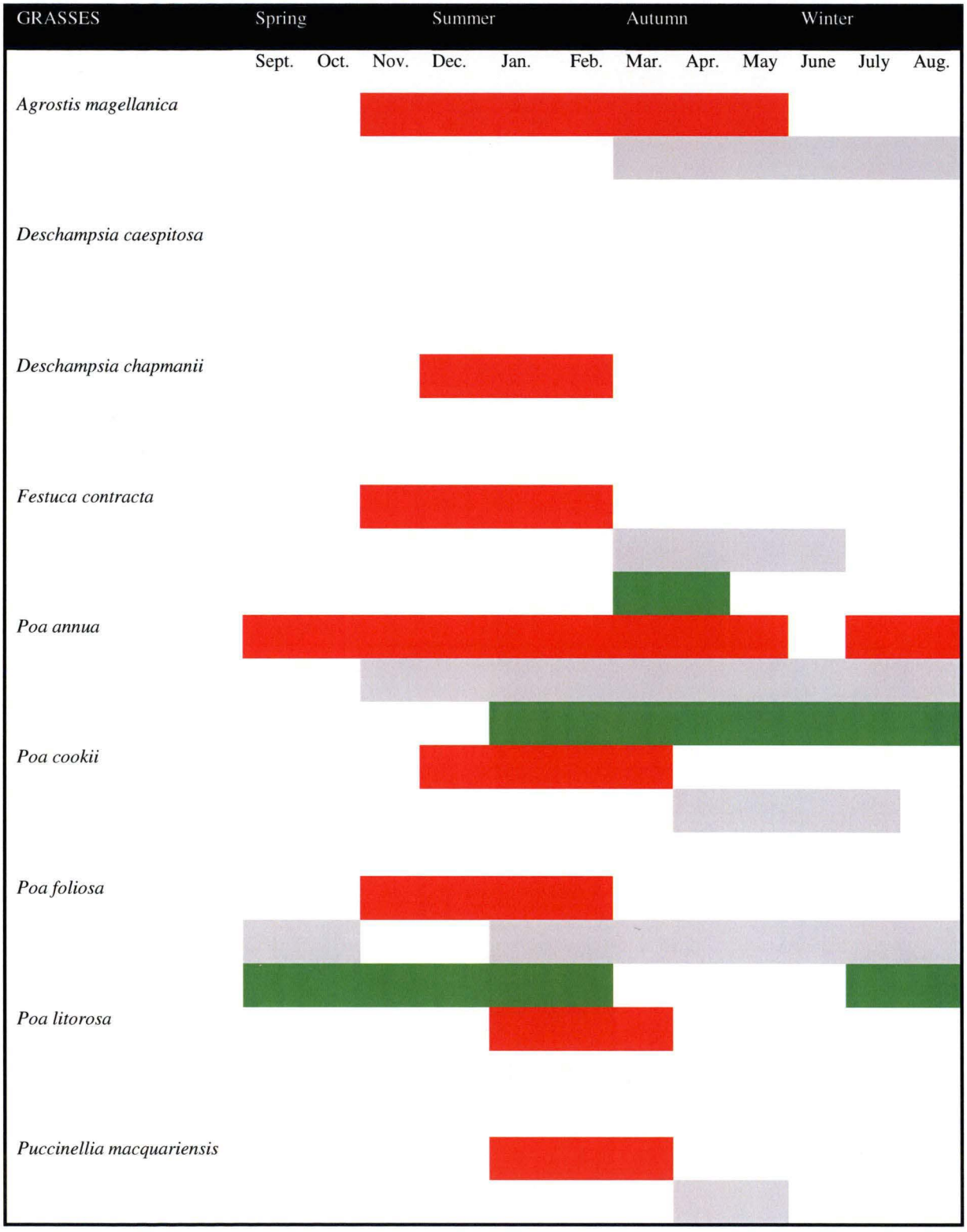


Seed rain on Macquarie I.

Introduction

Macquarie Island has never been connected to another land mass and therefore its vegetation is solely the result of long distance seed dispersal. However, nothing is known of seed dispersal within the island ecosystem. Understanding seed rain dynamics is important in understanding the distribution and variation in regional and local plant cover (Spence 1990a; Kalisz and McPeek 1993). As plants are generally sessile organisms, seeds, asexual propagules and plant fragments represent the only mobile mode of the terrestrial plant life cycle and this movement determines the ability of species to colonise new areas with seeds acting as founders of new populations. By influencing recruitment into local populations seeds affect population size, health and maintain genetic diversity (Silvertown 1987; Peart 1989). In order for seeds to germinate and establish they must first arrive at an appropriate microsite. Seed dispersal also reduces density-dependent mortality by moving propagules away from parent plants. (Hughes et al. 1994). However, several studies have shown that artic and alpine plants usually have short dispersal distances remaining close (<1 m) to parent plants (Silvertown 1987; Spence 1990b; Silvertown and Lovett Doust 1993; Scherff et al. 1994; Stocklin and Baumler 1996; Körner 1999). By dispersing close to parent plants, seeds of arctic and alpine plants have a higher likelihood of landing in a suitable microsite and, for some species, in a location where mycorrhizal infection is more likely to occur.

On Macquarie I. the major modes of dispersal are likely to be wind, water and gravity. Field observations indicated that many inflorescences simply 'dropped' their seeds on

to the vegetation or soil surface directly adjacent to the parent plant. The melting of snowbanks was also observed to disperse seeds. Once dispersed, seeds either germinate or contribute to a soil seed bank, which results from the accumulation of seed rain over one to several seasons. Previous studies on Macquarie I. have shown seed banks to be extensive containing numerous seeds of many species (Misiak unpub.). Seeds lie dormant in the soil until appropriate conditions for germination occur, however, nothing is known about seed longevity of these species. It is likely that moisture, freeze thaw events, fungal decay and inveterbrates affect seed longevity, further studies are needed.

Seed banks alone do not indicate the annual reproductive output of species or timing of species dispersal events. Therefore, to assess seed dispersal directly, seed traps were installed in several plant communities across Macquarie I. Seed traps allow direct determination of which species were dispersing seeds in a particular period. Thus, the aim of this study was to determine dispersal distances and periods for angiosperms on Macquarie I.

Materials & Methods

Seed rain was estimated using seed traps across eight sites with six traps deployed in each site. Traps were placed 1.5 m apart along a 7.5 m transect. Each trap consisted of a 10 cm wide by 20 cm long PVC tube that was forced into the ground such that the top of the tube was at the soil surface. The tube contained a 10 cm diameter plastic funnel with a nylon bag attached to the funnel base (as per Schott 1995). The bags were free draining and no water accumulated in the stocking bags except at the mire site where the ground water is at surface level. Bags were replaced every 5-7 weeks,

from March 2000 to March 2001 (except at two sites, Bauer Bay Beach and Lower Bauer Creek, where traps were not installed until late April). The surrounding vegetation was not disturbed by trap installation.

The contents of each bag were analysed under a dissecting microscope and the seeds identified to species, where possible, using field specimens and a seed atlas (Bergstrom 1986a). For each sampling period the contents of the six traps from each site were bulked to obtain an average number of seeds per species per site, which was then scaled up to give species of seed per m^2. Where *S. polaris* fruits were trapped, the number of fruits was multiplied by three to give a conservative estimate of seeds present as these fruits contain three or four seeds.

Sites

Eight sites of varying composition and structure were studied across the island (Table 2.5a and 2.5 b) and a map of the site locations is shown in Plate 2.8. Several sites were also utilised in other studies (Chapter 3, 4, 5). The commencement of trapping events varied between sites due to logistical and time constraints; however, most sites had traps installed in late autumn 2000. All traps were left in the field for 12 months, however, analysis proved time consuming therefore not all samples were processed. Table 2.5 indicates which months' samples have been analysed at each site. For all eight sites the first autumn samples were analysed. Priority was given to process samples from three seedling emergence sites (see Chapter 5). Four feldmark samples were also able to be processed due to the lack of material, thus making them quick to process. Time constrained further analysis of other seed rain form the remaining sites.

Species identification

All three species of *Colobanthus* have similar seeds as do *Acaena* spp. therefore the seeds of each genus were grouped unless there was an identified adult plant adjacent to or over hanging the trap, for example for short grassland traps surrounded only by *Acaena magellanica* plants it was assumed that any seeds within the traps were *Acaena magellanica*. *Poa* spp. were discernable as *Poa annua* seeds are smaller than those of *Poa foliosa*, and it was assumed than no *Poa cookii* seeds were trapped where there were no adult plants in the vicinity (>1 km) of any of the trap sites.

Disturbance

On several occasions rats or skuas destroyed traps, disturbing or removing contents and these samples were not included. At sites with higher rabbit densities traps were filled with soil and humic matter on several occasions and these samples were also excluded from the analyses. At one of the herbfield sites (S3), rats entered the traps and fed on the contents, specifically *S. polaris* seed. If the bag was intact only those seeds identifiable as individuals were counted and classified as damaged, all unidentifiable seed fragments were discounted.

Results

All traps caught seeds irrespective of month or site. A total of 24 species were trapped, with four species remaining unidentified. The total number of species trapped at each of the eight sites during the study ranged from 13 to five species. Table 2.5 shows the number of species trapped at each site.

Plate 2.8 Seed trapping sites on Macquarie I.

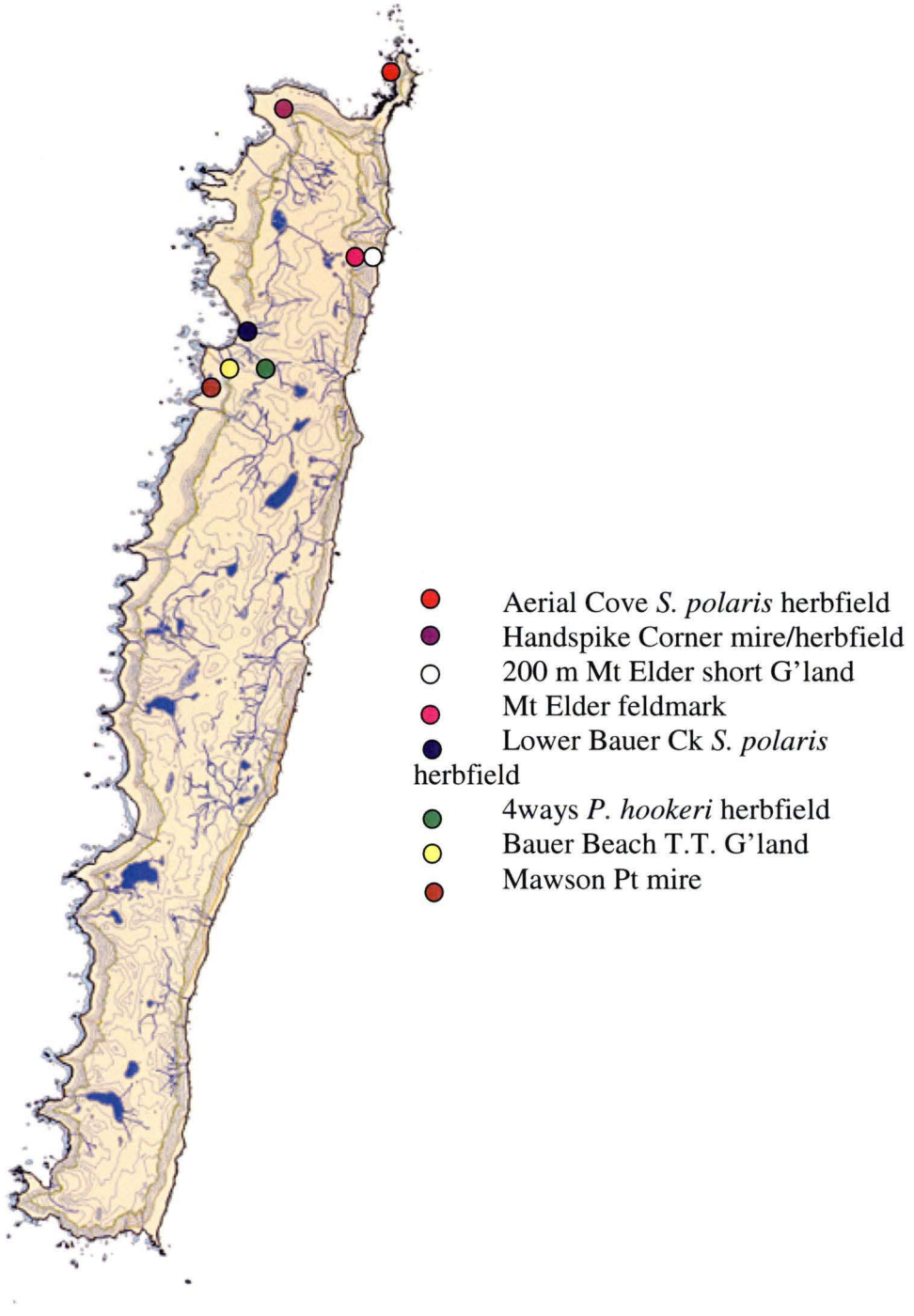


Table 2.5a. Site descriptions and seed rain across 4 sites (Handspike Corner, Aerial Cove, Four Ways, Lower Bauer Creek) where T.T. g'land = tall tussock grassland

Site Location and code	Handspike Corner (P1)	Aerial Cove (S3)	Four ways (P3)	Lower Bauer Ck (S2)
Vegetation community	Mire/ *P.hookeri* Herbfield	Herbfield	Herbfield	Herbfield/ T.T.g'land
Altitude (a.s.l.)	15 m	15 m	190 m	20 m
# spp. present in standing vegetation	12	6	8	10
% of standing vegetation trapped at site	64	100	72	60
# spp. present in seed rain over entire study	8	13	10	5
Max. spp. diversity in one trap event	6 (May)	6 (May)	9 (June)	4 (April & June)
Max. # seeds caught in one trap event	165 (March)	1260 (May)	2002 (April)	542 (June)
Dominant spp. in seed rain	*L. crinita*	*S. polaris*	*P. hookeri*	*L. crinita*
Unknown spp. of seed	0	3	0	0
Invertebrates found	-	Worms Spiders	Snails	-
Vertebrate disturbance	Skua	Rats Mice	Rats Rabbits	Rats Mice
Seeds caught but not present in the adjacent standing veg		*F. contracta* *L. plumosa* *U. hookeri* *M. fontana* *A. magellanica*	*S. polaris* *Colobanthus spp.* *M. fontana* *P. foliosa*	
Trapping events	March May July	April May June August January	April June August October	June October

Table 2.5b. Site descriptions and seed rain across 4 sites (Mt Elder-mid slope, Mt Elder-Plateau, Bauer Bay, Mawson Point) where T.T. g'land = tall tussock grassland

Site Location and code	Mt Elder -mid slope (S6)	Mt Elder -plateau	Bauer Bay	Mawson Pt.
Vegetation community	Short grassland	Feldmark	T.T. g'land	Mire
Altitude (a.s.l.)	200 m	365 m	15 m	10 m
# spp. present in standing vegetation	10		5	14
% of standing vegetation trapped at site	50	80	80	62
# spp. present in seed rain over entire study	11	5	8	9
Max. spp. diversity in one trap event	10 (April)	4 (April & June)	6 (July)	9 (April)
Max. # seeds caught in one trap event	974 (April)	135 (April)	187 (July)	437 (April)
Dominant spp. in seed rain	*L. crinita*	*L. crinita*	*P. foliosa*	*Agrostis magellanica*
Unknown spp. of seed	0	0	1	2
Invertebrates found	-	Snails Spiders	Snails	-
Vertebrate disturbance	-	-	Rabbits	Skua
Seeds caught but not present in the adjacent standing veg	*S. polaris*		*S. polaris* *L. plumosa* *M. fontana*	
Trapping events	April June	April June August January	July October	April

The *S. polaris* dominated herbfield had the most species trapped (13 spp.) while the feldmark and tall tussock grassland had the lowest number of species (5 spp.).

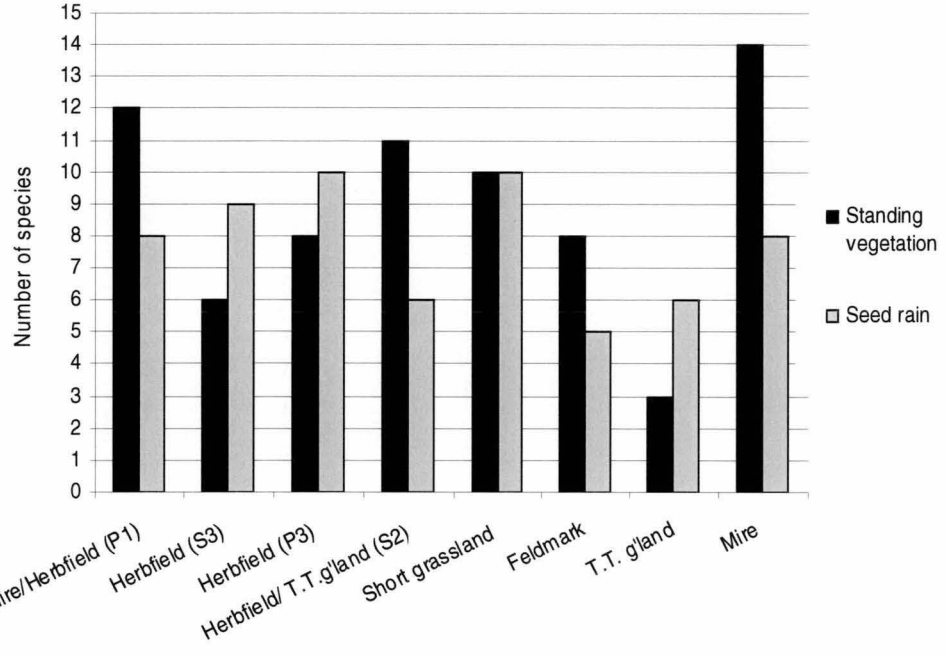


Figure 2.1 Total species richness of standing vegetation (black) and seed rain (shaded) at each site

Montia fontana and *Agrostis magellanica* were the most widespread species and seeds of these species were recorded at all sites except the tall tussock grassland (Figure 2.2a-h). *Luzula crinita*, was the most abundant of the sedges producing vast amounts of seed, across several sites (Figure 2.2a-h). The occurrence of an individual or several inflorescences within a trap drastically increased *L. crinita* seed density for the site. *Azorella macquariensis* was only trapped at the feldmark site (Figure 2.2a-h) where it had low densities (33 seeds m^{-2}). Seed rain density (seeds m^{-2}) varied across sites for each species.

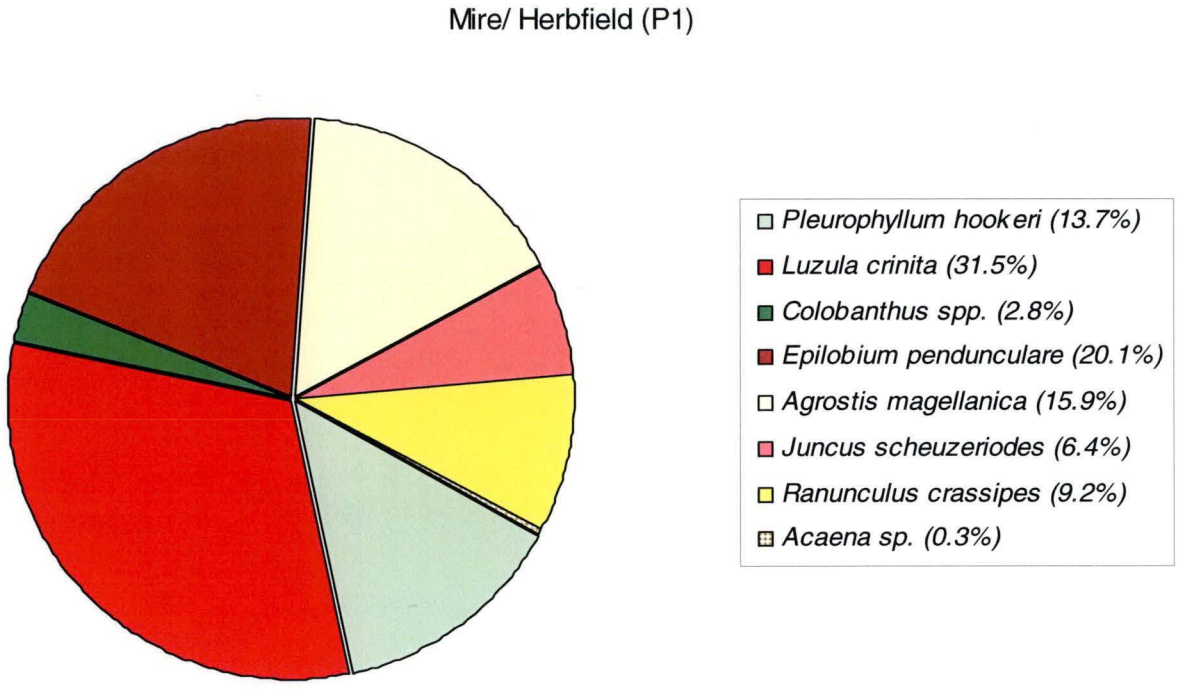


Figure 2.2a Seed rain composition of a mire/*P. hookeri* herbfield community

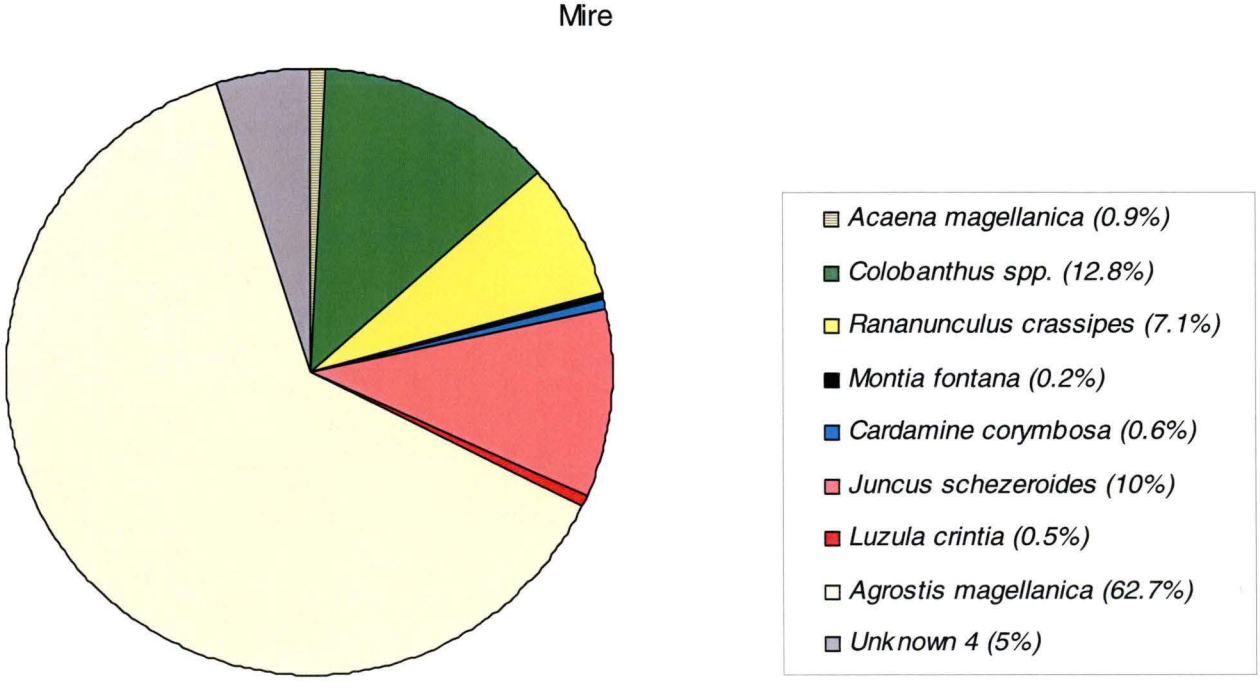


Figure 2.2b Seed rain composition of a mire community

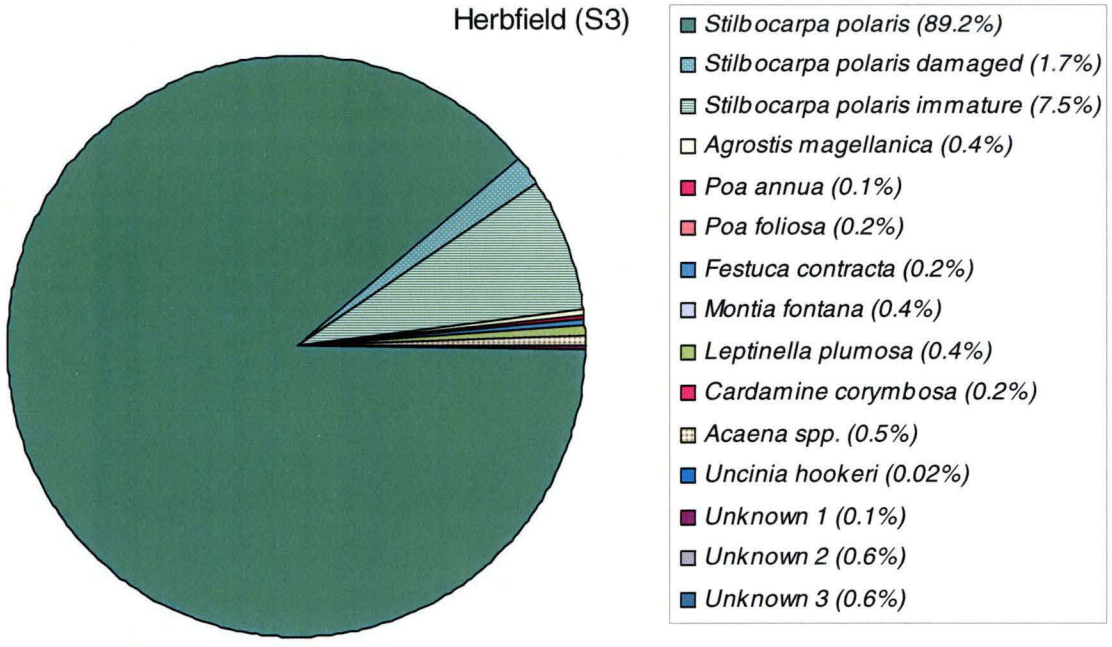


Figure 2.2c Seed rain composition of a *S. polaris* herbfield.

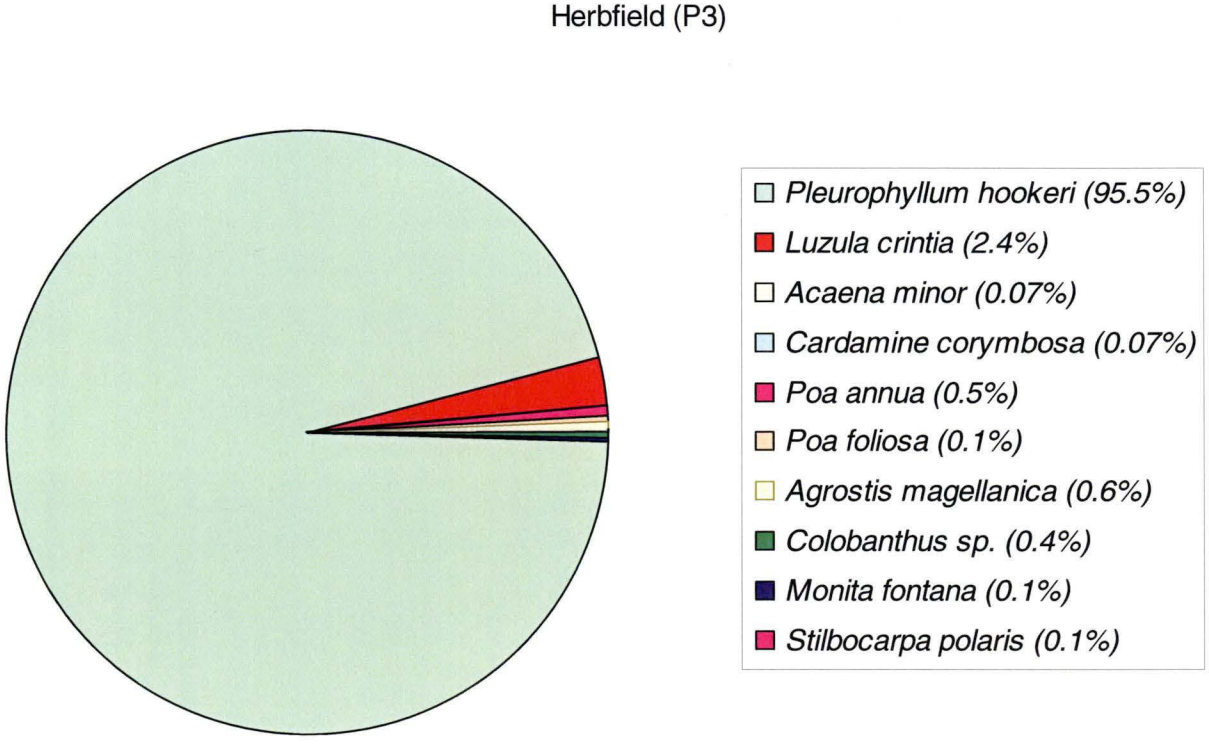


Figure 2.2d Seed rain composition of a *P. hookeri* herbfield.

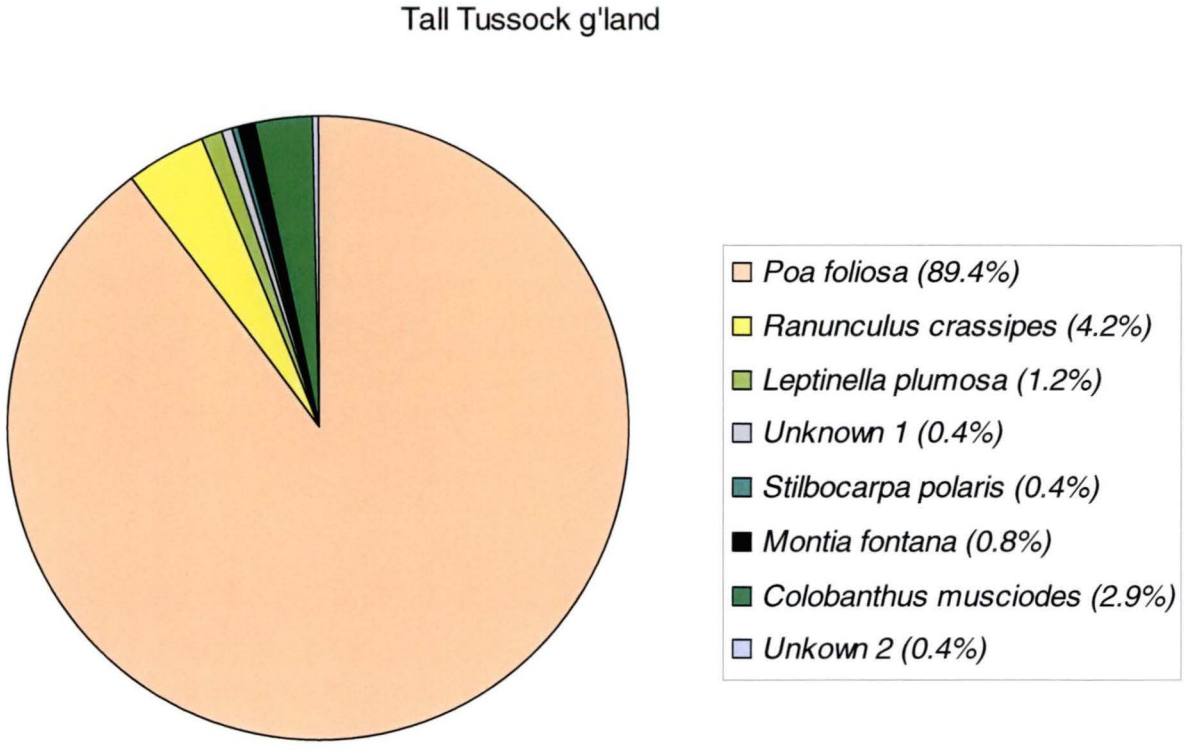


Figure 2.2e Seed rain composition of a *Poa foliosa* dominated tall tussock grassland.

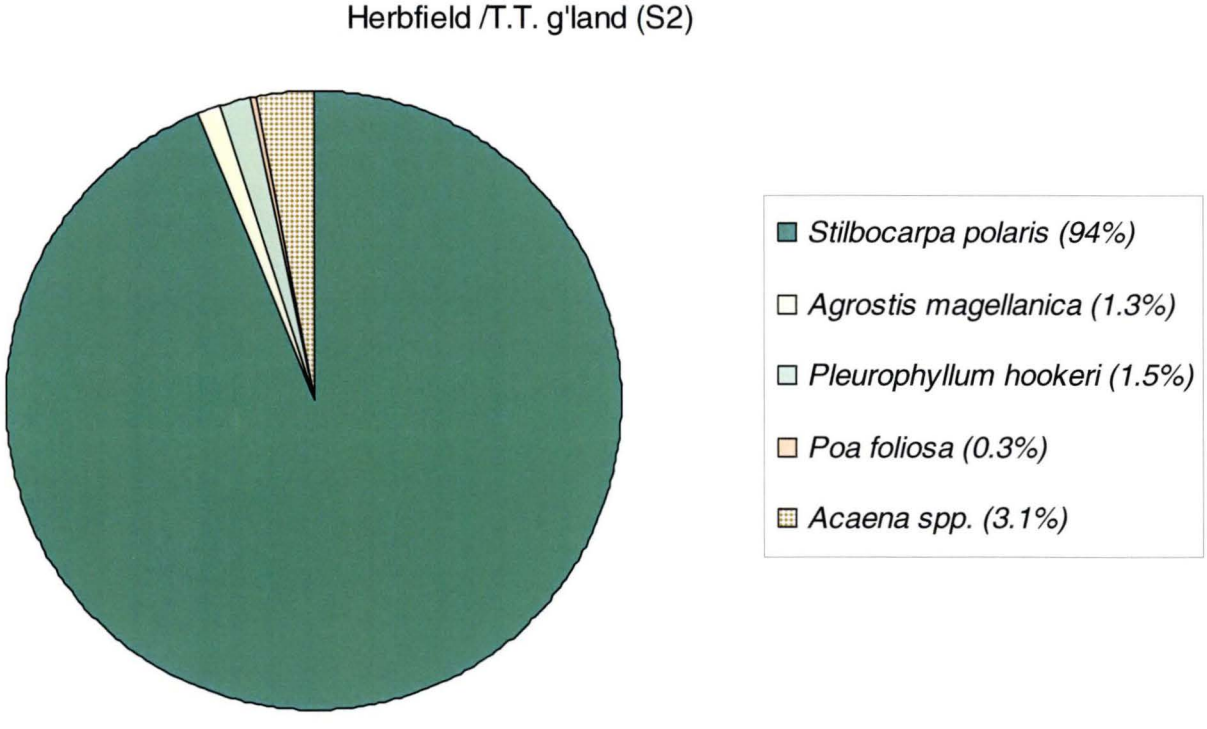


Figure 2.2f Seed rain composition of a mixed herbfield/tall tussock grassland.

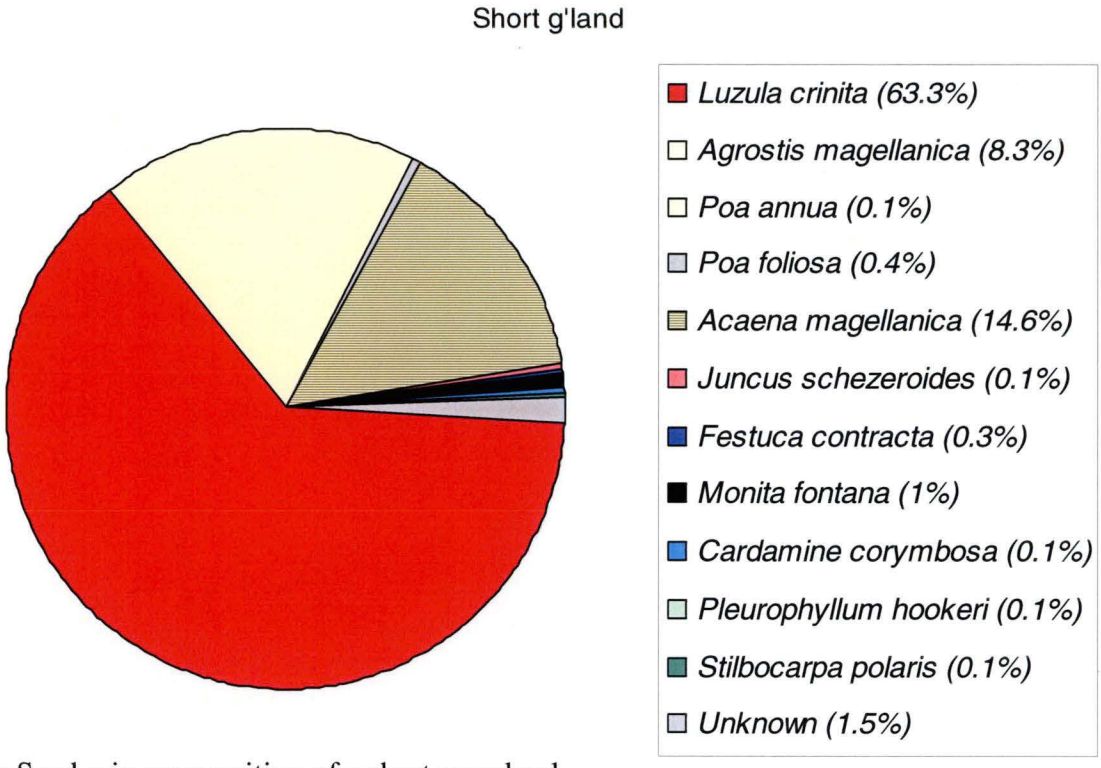


Figure 2.2g Seed rain composition of a short grassland.

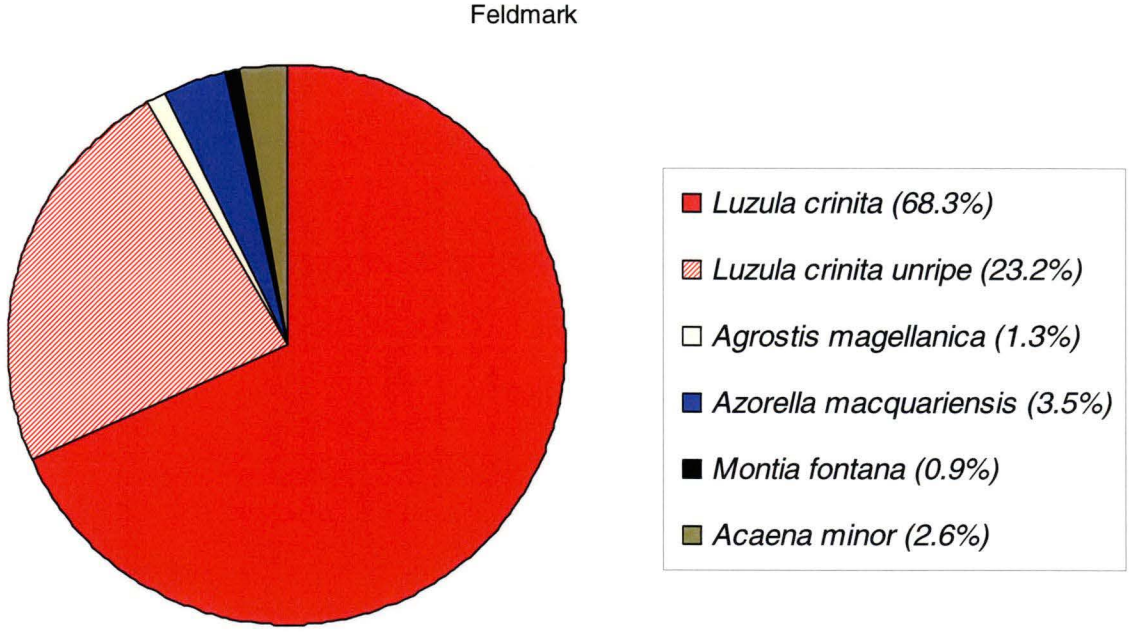


Figure 2.2h Seed rain composition of a feldmark community.

Within herbfield communities megaherbs (*P. hookeri* and *S. polaris*) dominated seed rain, and similarly in tall tussock grasslands *Poa foliosa* dominated seed rain (Figure 2.2a-h.). At all sites the dominant species in the standing vegetation dominated the seed rain, the only exception being at the mire/herbfield (P1) site where *Coprosma perpusilla* was co-dominant with *P. hookeri* in the vegetation but was absent from the seed rain.

Figure 2.3 shows the mean seed rain of both megaherbs over several trapping events. The greatest seed rain event for a species was *P. hookeri* in a herbfield (total of 13,339 seeds m^{-2}) during the April trap event, followed by *S. polaris* (total of 10, 009 seeds m^{-2}) in May. Figures 2.4a-d show the maximum recorded mean seed density of a trapping event for each species recorded at each site where the species was detected. The figures show that *L. crinita, Agrostis magellanica, Acaena magellanica,* all produced a mean seed rain of over 1000 seeds m^{-2} at a site in one or more trapping periods (6-7 weeks).

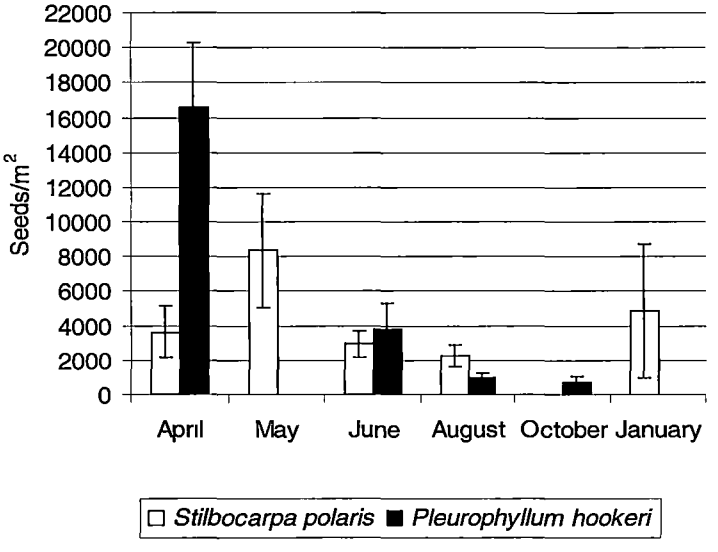


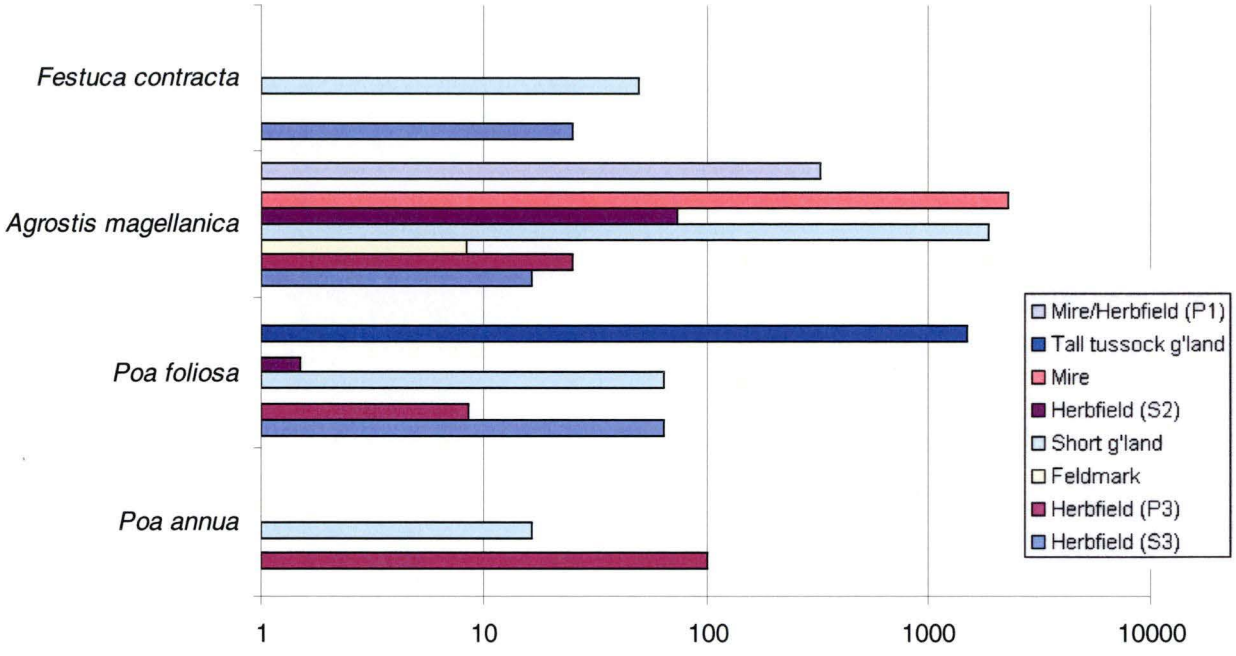
Figure 2.3 Seasonal seed rain of megaherbs (*P. hookeri* and *S. polaris*). Error bars show standard error

Figure 2.1 shows the number of species in the standing vegetation compared to the number of species in the seed rain, while Table 2.5 indicates the proportion of the species in the standing vegetation that had seeds present in the seed rain. Table 2.5 also indicates species which had dispersed seeds into the traps yet were absent from the standing vegetation immediately adjacent to the traps. Eight species had seed that was identified in traps at a site despite its absence from the adjacent standing vegetation.

For the seeds that were unidentifiable it is likely that one unknown group consisted of old weathered *Acaena* spp. seeds due to their distinctive three pronged apex. The other three unidentified seed types (considered three species) may also be from weathering or damage to other species of seeds present. If seeds remained in the soil seed bank it is possible that they change colour and shape once the endocarp is eroded.

The following seven angiosperm species were not detected in seed traps despite growing at several sites: *Coprosma perpusilla, Hydrocotyle novae-zeelandae, Callitriche antarctica, Isolepis aucklandicus, Stellaria media, Cerastium fontanum, Deschampsia chapmanii.* The remaining 8 species were not growing in the vicinity of the trap sites and consequently were not detected in any traps: *Uncinia divaricata, Stellaria parviflora, Deschampsia caespitosa, Poa litorosa, Poa cookii, Carex trifida, Galium antarctica, Nematocerus dienema.*

a) Grasses



b) Sedges

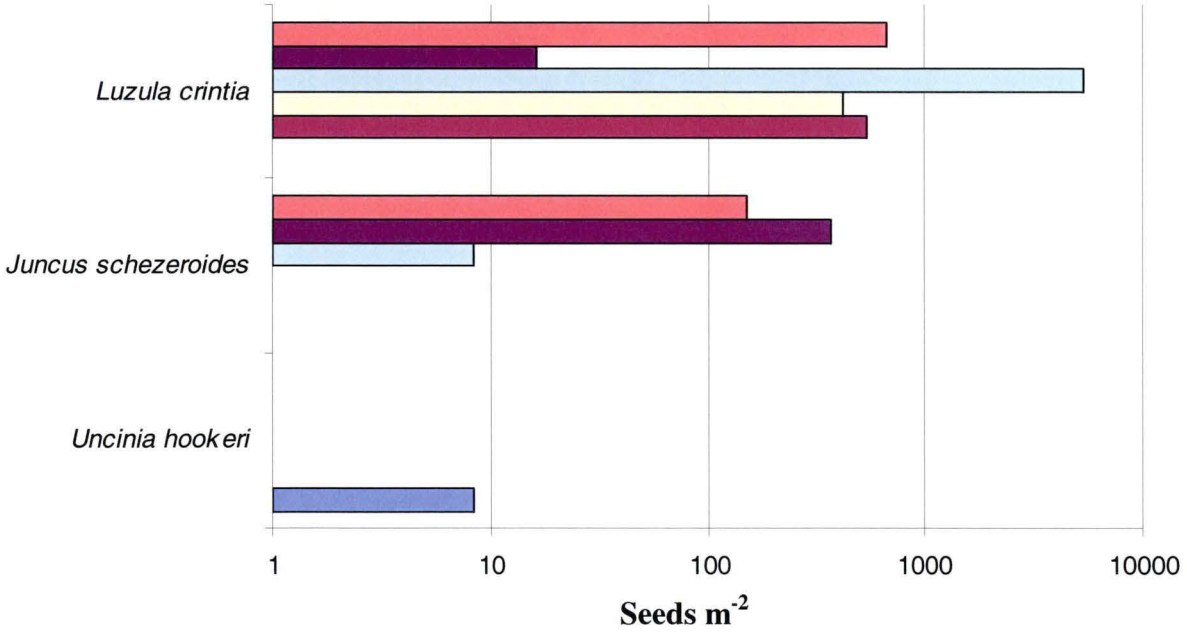
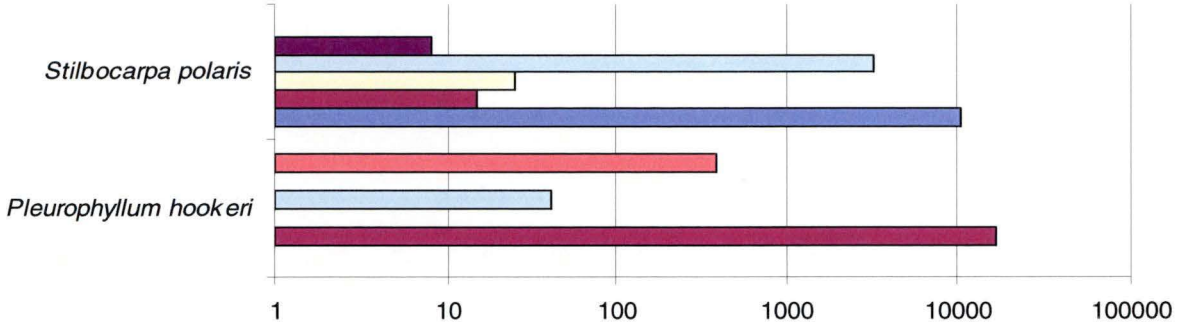


Figure 2.4 a & b. Maximum mean seed density trapped at each site within one trapping event (6-7) weeks. Different colours indicate different sites. Note logarithmic scale on x-axis.

c) Megaherbs



d) Small herbs

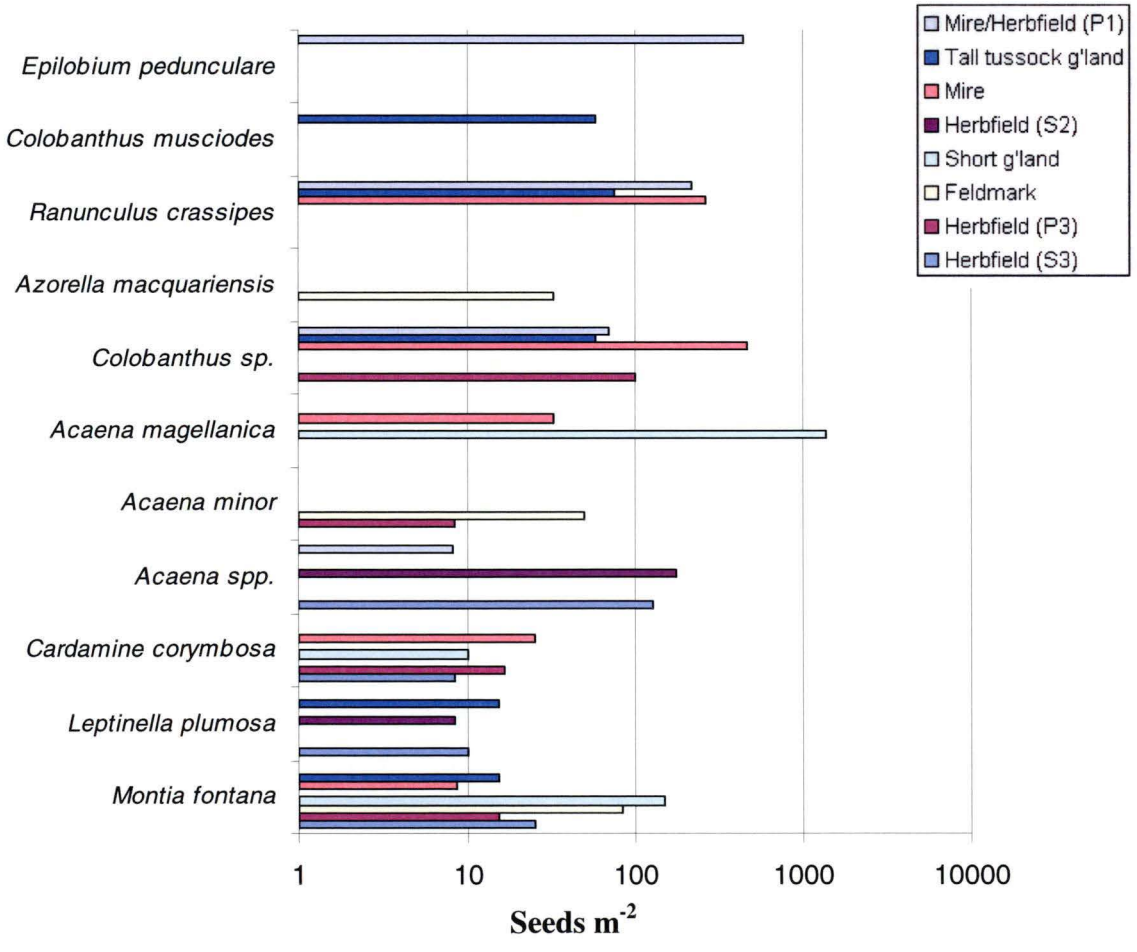


Figure 2.4 c & d. Maximum mean seed density trapped at each site within one trapping event (6-7) weeks. Different colours indicate different sites. Note logarithmic scale on x-axis

Discussion

This preliminary study shows that seeds of numerous species are dispersed into all plant communities throughout the year. The amount of seed deposited by dominant species was high. Prior to this study the only research conducted on seeds on Macquarie I. found that there were considerable amounts of seed within the soil seed bank (Misiak unpub.). However, nothing was known of dispersal times and there was no indication of how much seed enters a community at a given time. The results show that the majority (<60 %) of subantarctic species produce and disperse seeds.

This study has identified seed dispersal times for the three dominant species on the island; *P. hookeri*, *S. polaris* and *P. foliosa,* showing there is a distinct seasonality in dispersal. Seed rain was spatially patchy with some traps collecting numerous seeds of a species and other nearby traps collecting none, as has been found in other studies (Spence 1990b). This was particularly evident at both herbfield sites where large inflorescences simply fall on top of traps resulting in numerous seeds being deposited, while 1.5 m away few seeds were caught, indicated by the large error bars in Figure 2.3.

Widespread and abundant species in the island's vegetation, such as *Luzula crinita, Agrostis magellanica* and *Acaena* spp., were readily detected in the seed rain at most sites. In contrast, *Azorella macquariensis* was only collected from high altitude feldmark communities. The more abundant a species the more prevalent their seeds will be, indicating that although these species expand through vegetative growth they also have abundant seed rain which may result in population recruitment. Overall, the seed rain at each site was representative of the standing vegetation, with all sites

having over half of the species in the standing vegetation identified in traps. Four of the eight sites had greater than 70% of the standing species trapped, with one herbfield site (S3) having seeds of all species present and additional species, caught in traps during the study. Interestingly this is the site for which the most samples were analysed and this may explain the 100% detection of the standing vegetation in the seed rain.

The study also showed that some species were dispersing into the site, as they were trapped as seeds but not detected in the standing vegetation. However, most of these species were within 15 m of the traps and despite thorough searching some smaller species may have gone undetected, as all sites were densely vegetated (herbfields or tall tussock grassland). Two larger species and therefore more detectable species, *Stilbocarpa polaris* and *Uncinia hookeri,* were trapped at sites where neither species was present or nearby (>250 m) which has implications regarding their dispersal modes. *Uncinia hookeri* seeds are barbed and it is possible that that an animal transported the seed to the herbfield (S3) traps. As previously discussed the wind blown dried inflorescences of *S. polaris* were observed in areas where the species does not grow, although not a very common occurrence it may explain the presence of *S. polaris* in the herbfield (P3). Although *S. polaris* fruits are large compared to other seeds, and wind blown dispersal has never been observed. It should not be discounted as a vector for dispersing fruits.

The two megaherbs produce vast quantities of seeds and the seed rain densities for both species are higher than similar seed rain studies in alpine or arctic communities. Stocklin and Baumler (1996) reported a maximum of 1945 seeds/4.12 m^2/95 days

(calculates approximately to 1794 seeds/m^2/year) for a small herb in the Swiss Alps. Urbanksa and Fattorini (2000) investigating restoration ecology of high alpine communities in the Swiss Alps measured a maximum seed rain for a site of 3557 seeds/m^2/year consisting of three species of small herb. Molau and Larsson (2000) studied seeds rain in alpine communities of Swedish Lapland obtaining a maximum seed rain at a site of 1362 seeds/m^2/year comprising 11 species. Spence (1990a) obtained a maximum of 8871 seeds/m^2/2 years (approximately calculates to 4435 seeds/m^2/year)in a alpine community in New Zealand. Obviously the reproductive output of plants on Macquarie I., in particular the megaherbs, is far greater than any plants in these alpine and arctic communities, with *P. hookeri* having a seed rain of 13, 339 seeds/m^2/42 days and *S. polaris* 10, 009 seeds/m^2/35 days. Seed rain values for the arctic and alpine studies are given in seeds/m^2/year, while the annual seed rain for megaherbs was not calculated, *S. polaris* and *P. hookeri* dispersed far more seed over a shorter duration (ie. 35 and 42 days) than any of these previous studies. Even the common small herbs dispersed more than their arctic and alpine counterparts of the above mentioned studies.

The pappussed seeds of the megaherb *P. hookeri* did not disperse very far from the parent plant. Pedicels were often still attached to parent plants after the seeds had been deposited on the ground beneath them. Several species, such as *Epilobium brunnescens, Epilobium peduncluare, Ranunculus crassipes, Agrostis magellanica,* were also observed to have seeds massed on the ground surrounding the adult plants. During the study *Acaena spp.* seeds were seen adhering to skua, petrel and albatross feathers and rabbit fur, even rabbit carcasses which were moved around the island by scavenging skuas were observed covered in *Acaena* seeds. It is likely that other

species with seeds with hooked, barbed or sticky seeds, such as *U. hookeri, U. divarcata* and *L. plumosa* could also be transported around the island by birds and animals.

Absent species

Fifteen flowering species that occur on the island were absent from the seed rain. It was not expected that the spores of the five fern and fern allies would be detected, nor the three species which are extremely restricted in distribution. Of the remaining species, eight are rare (Copson 1984) and were not present in the communities where trapping occurred. Species that were present and not detected in the seed rain were *Coprosma perpusilla, Callitriche antarctica, Hydrocotyle novae-zeelandae, Isolepis aucklandicus, Stellaria media, Cerastium fontanum, Deschampsia chapmanii,* all of which were flowering at the sites. These species either were not dispersing seeds at the time of trapping or may have been classified as an unknown species, although this is unlikely for *Cerastium fontanum* and *Coprosma perpusilla* as they have distinctive seeds. It is possible that the restricted period for which seed rain was analysed means that the dispersal period of these species was missed. It is unlikely seeds were too small to be detected by a dissecting microscope. Unlike some of the species trapped (for example *Pleurophyllum hookeri, Acaena* ssp., *Epilobium* ssp.) none of the species absent from the seed rain have specialised appendages or explosive capsules to aid seed dispersal. It is possible that this restricts their dispersal ability.

Coprosoma perpusilla has large, round (approximately 7 mm in diameter) fleshy, red fruits. These fruits remain attached to the adult plant for over two years, suppressed below the leaves of the prostrate mat formed by the plant, and is therefore unlikely to

be wind or water dispersed. During the study a bird regurgitate containing over 100 seeds of the plant and red fruit flesh was found in the vicinity of the plant at the site where it grew (mire/herbfield P1) in late winter. Although no birds have ever been observed removing fruits from *C. perpusilla* the presence of penguin feathers and shells of an inshore marine gastropod in the regurgitate suggest either that a kelp gull (*Larus dominicanus*) or a skua (*Catharacta skua*) consumed the fruits. It is not known what role this may play in the species' seed dispersal.

Disturbance

Rat scats were found in several traps and there was evidence of considerable scratching and digging at the site throughout the study. During winter they were feeding on a substantial proportion of *S. polaris* fruits. It was not possible to quantify what proportion of seeds were damaged as many seeds were fragmented beyond recognition. It is therefore likely that values of *S. polaris* seeds given for this site are underestimated. The results for *S. polaris* in January are unnaturally high due to rat disturbance at the site. Digging and scratching by rats resulted in previously dispersed seeds (from the previous winter months) that had been lying on the ground, being deposited into traps. At the same time undisturbed traps contained very few seeds, as indicated by the large standard errors.

The study has shown that rats act as small scale dispersal vectors by disturbing the soil surface and consequently dispersed seed. There was evidence of mice grazing on seeds as some small seed caches were found amongst the vegetation surrounding traps, containing *Agrostis magellancia*, *F. contracta*, and *L. crinita* inflorescences, as has previously been observed (Copson 1986). Rabbits were also found to create

similar disturbance at other sites particularly in the tall tussock grassland where they regularly filled traps with sand through digging. The study has therefore shown that introduced vertebrates alter seed rain processes by consuming and burying seed post dispersal thus limiting species recruitment potential.

This preliminary study has shown that flowering and seed dispersal of flowering plants on Macquarie I. are seasonal, with most plants flowering in spring and summer and dispersing fruits in late autumn and early winter. Seed rain at most sites was representative of the majority of the standing vegetation, with the most widespread and abundant species on the island being the most widespread and abundant species present in the seed rain. Seed dispersal is important for ensuring the establishment of new individuals and this study has shown that several of the species produce large numbers of seeds, which are then dispersed into communities. The density of seed rain measured is greater than seed rain values previously recorded in arctic and alpine studies. Megaherb species deposited the most seeds during the study which may explain their widespread distribution and domination of the island's vegetation. *Stilbocarpa polaris* was found to have wide dispersal abilities with seeds being caught at sites where it did not grow. *Poa foliosa* also dominates the island's coastal slopes and in the tall tussock grassland it too was shown to have high seed rain with over 1000 seeds/ m^2/ month dispersed during winter, several months after flowering had ceased. This is the first study to investigate seed rain of Macquarie I. plants and has shown that many species produce vast amounts of seeds which then disperse providing the potential for future recruitment.

Chapter 3 – Biomass Allocation in Megaherbs

Introduction

Megaherbs are 'herbaceous perennial forbs that have large growth forms with large leaves and very colourful floral displays' (Hooker 1844). The occurrence of this unusual group of plants in the subantarctic has been discussed by several researchers (Hooker 1844; Jenkin and Ashton 1979; Meurk 1982; Wardle 1991; Körner 1999; Mitchell et al. 1999; Nicholls and Rapson 1999). Subantarctic islands support relatively simple ecosystems principally due to geographical isolation and harsh climates (Lewis-Smith 1984). The flora of the subantarctic is depauperate and characterised by low plants lacking woody tissue. Bryophytes, tight compact cushion plants and dense tussock grasses dominate in subantarctic communities. Such growth habits enable these plants to grow in a cold, windy, low light environment. The presence of megaherbs in the subantarctic is intriguing as they are foliose, creating a large surface area and they produce numerous, large inflorescences, unlike most other subantarctic plants that are small in height and biomass.

Large leaved forbs are not globally rare, as they are found in warm temperate and subtropical semi-deserts, in the lowland and montane humid tropics, the tropical alpine zone as well as in temperate climates. They are a taxonomically diverse group including the genera *Gunnera* (Chile), *Espletia* and *Puya* (Andes), *Argyroxiphium* (Hawaii), *Lobelia* and *Dendrosenecio* (Kenya) (Nicholls and Rapson 1999). There are several species occurring on mainland New Zealand and offshore islands, such as

Ranunculus lyalli, *Anisotome lyalli*, *Myosotidium hortensia* (Nicholls and Rapson 1999). Megaherbs also form a significant component of subantarctic vegetation.

Subantarctic megaherbs

Megaherbs occur on the Southern Ocean islands of Crozet, Kerguelen, Heard, Marion, Macquarie, Campbell and the Auckland Is. These subantarctic megaherbs come from four families: Apiaceae, Asteraceae, Brassiceae, Liliaceae. The genera *Pleurophyllum* Hook.f., and *Stilbocarpa* (Hook. f.) Decne. & Planch., contain only macrophyllous forbs and are restricted to Macquarie I. and the Southern Oceanic islands of New Zealand. The genus *Pleurophyllum* contains three species; *P. speciosum, P. criniferum* and *P. hookeri*. The genus *Stilbocarpa* comprises three species; *S. robusta, S. lyalli, S. polaris*. Both genera are endemic to the New Zealand Southern Ocean islands archipelago, and Macquarie I. with an approximate latitude range of 47°S to 56°S. At lower latitudes (Campbell and the Auckland Is.), the megaherbs compete with shrubs and woody species. Macquarie I. is the southernmost extent of both genera, with only one species of each occurring there. *P. hookeri* and *S. polaris* dominate the island vegetation along with the tussock grass *Poa foliosa.*

Megaherb strategies for survival

Many studies examine the structure and function of novel species in extreme environments, such as deep oceans, mountain tops and deserts (Vuilleumier and Monasterio 1986; Rundel and Witter 1994). By looking at plant performance at their limits, their physiological and life history strategies can be better understood. Moore (1979) suggested that the sporadic occurrence of *Pleurophyllum* and *Stilbocarpa*

across the islands of southern New Zealand indicates that these sites are refugia reflecting the massive extinction of a pre-Pleistocene family.

Mitchell et al. (1999) proposed that most megaherb species have evolved from small to giant forms, thus being derived from a more modest ancestor growing in surrounding lowland forests or grasslands. The strong contrast between megaherbs and surrounding low stature grass and shrub vegetation has attracted biologists for many years (Jenkin and Ashton 1970; Jenkin 1972; Moore 1979; Cuatrecasas 1986; Mabberley 1986; Rundel and Witter 1994; Hennion and Walton 1997b). Such contrast is evident between megaherbs and surrounding species on Macquarie I. The dominance of this unusual growth form is intriguing and prompts consideration of what adaptive strategies these plants have developed enabling them to proliferate and dominate so many of the island's communities.

Snow accumulation and wind abrasion can limit plant growth, wind also damages buds, flowers and vegetative organs thus lowering photosynthetic and reproductive ability in plants (Brancaleoni et al. 2003). Strong winds on the upland plateau of Macquarie I. influence evapotranspiration (Tweedie 2000) as well as having potentially damaging effects. Under these climatic conditions, large leaves would not appear to be advantageous, but several researchers have proposed that this habit is indeed beneficial in the subantarctic environment. Wardle (1991) suggested that the large leaves harvest heat and light in this typically low light environment, by acting as solar panels and focusing radiation inward to the growing apex of the plant. Jenkin and Ashton (1970) stated that the large leaf area is for the interception of the predominantly diffuse light. They stated that high chlorophyll contents, high leaf area

indices, sustained leaf production throughout the year and leaf longevity are adaptations to the low light environment, and incident energy appears to be utilized efficiently. Meurk et al. (1994a) suggested that the large leaves intercept marine aerosols containing nutrients. Nicholls and Rapson (1999) suggested that the rosette form reduces the detrimental effects of the subantarctic temperature and winds, and that large leaves may aid in competition with surrounding species. Even if all of these functions are true, the large leaf size of megaherbs makes them susceptible to grazing (Meurk et al. 1994b). The absence of native vertebrate herbivores on these islands no doubt contributes to megaherbs being able to survive and dominate. The Macquarie Island populations of both species *P. hookeri* and *S. polaris* are the most extensive in the world.

The aims of this study were:

- To identify some physical characteristics that define a megaherb
- To investigate how megaherbs allocate their resources
- To investigate the structural differences between the two species under the same island environment
- To investigate any intraspecific variation across sites

Plate 3.1 A & D Megaherb leaves in dense herbfields. *S. polaris* pictured top, *P. hookeri* pictured bottom. B &C Large leaf area make megaherbs susceptible to snow and ice accumulation.

Species descriptions

The complex taxonomic history of *Stilbocarpa* was discussed in Mitchell et al. (1999). Collected by Hooker on the Antarctic expedition of the James Clark Ross expedition of 1840, the species was initially described as *Aralia polaris* (Araliaceae). Hooker (1844) described it as "one of the most handsome and singular of the vegetable production in the group of islands in which it inhabits, which certainly contains a greater portion of large and beautiful plants relative to the whole vegetation than any country with which I am acquainted". He later proposed the sectional name *Stilbocarpa*, retaining it in the genus *Aralia*. Recent phylogenetic studies by Mitchell et al. (1999) found that *Stilbocarpa* is more closely related to herbaceous species within the family Apiaceae than to those in Araliaceae, and suggested its possible ancestors could be the tiny *Schizeilema* or *Azorella*.

Stilbocarpa polaris (Hombr. & Jacquinot ex. Hook. F.) A. Gray forms terminal rosettes that emerge from thick, fleshy rhizomes (Mitchell et al. 1999). *S. polaris* grows as high as 1.8 m at sheltered coastal sites. Hnatiuk (1993) described the species' fleshy rhizome as being 4 cm diameter and up to 60cm long, with annular rings. Field observations indicate that rhizomes of this species can grow up to 1 m long, and 12 cm in diameter. The petiole is hollow, sheathing and sparingly to densely covered with coarse stiff hairs (Tweedie 2000).

S. polaris is widespread and abundant on coastal slopes around Macquarie I., occurring also along inland drainage channels and in isolated places on the plateau (Skotnicki et al. 2003). However, the species is stunted on the plateau and it has not been observed flowering above 300 m. a.s.l. *S. polaris* leaves persist through the

winter, however, the majority of growth, and rapid leaf expansion occurs during late spring and summer. Plants have maximum leaf area in late autumn and early winter (Tweedie 2000).

The lateral inflorescence of *S. polaris* is a large, globose, compound umbel that bears greenish-yellow flowers (Mitchell et al. 1999). *S. polaris* flowers annually, with flowers emerging in late spring and fruits ripening by late autumn, with most seed dispersing in early winter (see Chapter 2). The majority of fruit are deposited in large dense heaps immediately beneath or adjacent to the adult plant. (see Plates 3.2, 3.3, 3.4)

Plate 3.2 *Stilbocarpa polaris* plants with several young inflorescences. December 2000

Plate 3.3 *Stilbocarpa polaris* leaf detail showing trichomes laden with moisture

Plate 3.4 *Stilbocarpa polaris* inflorescence with fruit begin to ripe. March 2000.

Plate 3.5 *Pleurophyllum hookeri* rosettes in a dense mid altitude herbfield (Stony Creek in the background). December 2000

Plate 3.6 Single *Pleurophyllum hookeri* inflorescence. Photo Aleks Terauds

Plate 3.7 Senescent *Pleurophyllum hookeri* in winter. July 2000.

Pleurophyllum hookeri Buchan. is a large composite that grows up to 75 cm in diameter and height with extensive rhizomes up to 80cm in length. Plants are semi-deciduous with leaves reducing to a mound of decaying matter around the rosette in autumn. The dead leaves decompose over winter and contribute to the peaty soil beneath the rosettes. Expansion of new leaves occurs in late spring.

P. hookeri-dominated herbfields typically occur on waterlogged peat soils from near sea level up to 340 m a.s.l., but may also be found on sandy soils and in feldmark. Jenkin and Ashton (1979) found that the presence of air canals (presumably aerenchyma) in *P. hookeri* roots varies with the degrees of waterlogging, thus enabling the species to occupy a wide range of habitats. Patterning varies in *P. hookeri* and the species' distribution can be regular, clumped or random (Taylor 1955; Jenkin and Ashton 1979), depending on environmental factors such as drainage, wind exposure and temperature. Competition from associated vascular and bryophyte taxa also influences patterning, as well as affecting the balance between sexual and vegetative reproduction (Jenkin and Ashton 1979). *P. hookeri* exhibits semi-masting behaviour on Macquarie Island with profuse flowering occurring every two to three years (Jenkin and Ashton 1979) and flowers being extremely rare in other years. In a mass flowering year, all populations over the island flower, regardless of elevation, aspect, soil type and water availability.

Major flowering events result in the release of vast quantities of fruit (see Chapter 2) during mid to late autumn, the exact timing depending on altitude. The majority of fruits are dispersed when peduncles dry and fall due to the combined fruit weight.

Once shed, wind and water further disperse the stiff, pappused fruits (see Plate 3.5, 3.6, 3.7).

The two megaherbs do have differing fruit structures. *S. polaris* fruit contain up to 4 small seeds within a hard fleshy coat and *P. hookeri* fruits are single seeded fruits characteristic of Asteraceae. *S. polaris* fruits are heavier and are subtended on long pedicles (up to 1m long) and peduncles. *P. hookeri* fruits are amassed on capitula supported by thick pedicels (up to 75cm high).

Materials and Methods

Site Description

Stilbocarpa polaris plants were collected from three 20 x 20 m sites in the northern third of the island, in March 2002 (Plate 3.8). Two sites, Aerial Cove and Bauer Creek, were *Stilbocarpa*-dominated tall tussock grasslands at 15 m and 20 m a.s.l., respectively. Aerial Cove (S3) had a westerly aspect while Lower Bauer Creek (S2) had a south-westerly aspect. The third site, Mt Elder (S6) had an easterly aspect and was an ecotone between tall tussock grassland and short grassland at 200 m a.s.l. It appears to be a seral community recovering from intense rabbit grazing in the past (Tweedie 2000).

Pleurophyllum hookeri plants were collected from six sites across the island (Plate 3.8). The Windy Ridge site (P7) was a feldmark dominated by *Azorella macquariensis* and *P. hookeri*. Occurring at 360 m a. s. l. with a north westerly aspect,

the site was in a gully on an extremely exposed plateau ridge consisting of rocky mineral soils (see Plate 3.9).

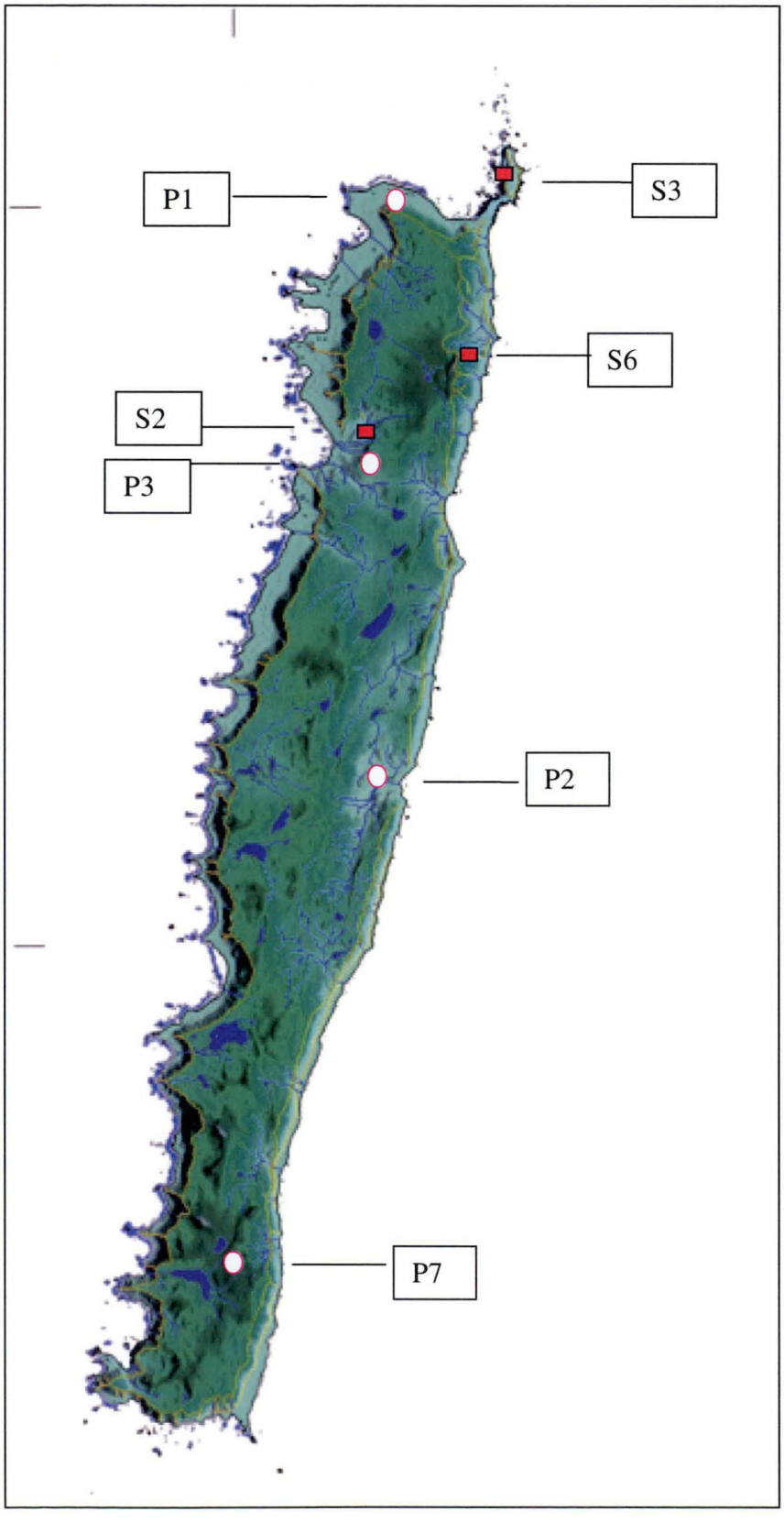


Plate 3.8 Map of Macquarie I. showing study sites

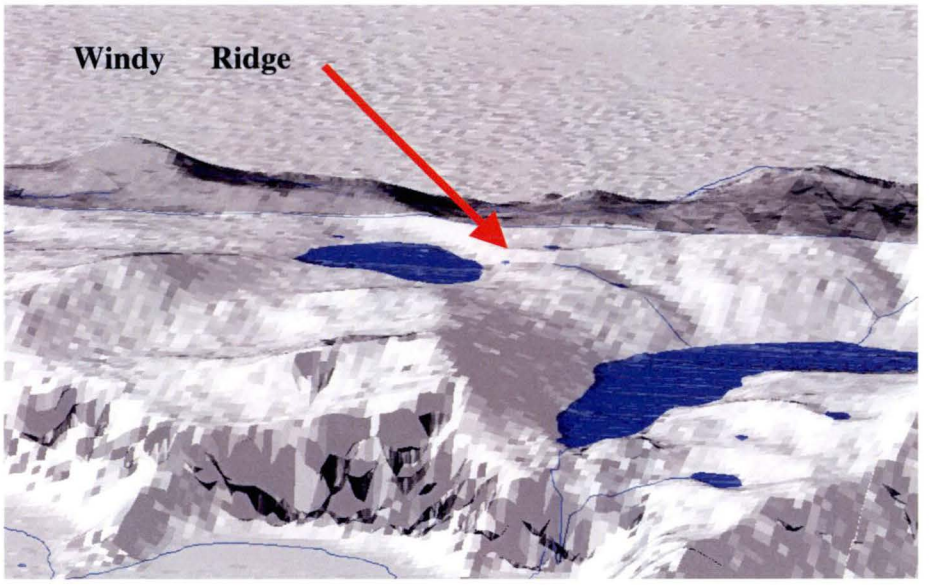


Plate 3.9 P7 at Windy Ridge looking east across the island, with Waterfall Lake to the south. Data courtesy of the Australian Antarctic Datacentre and NASA.

The second site (P3) was on the upper south-west facing slopes of the Stony Creek valley (see Plate 3.10). At 190 m a. s. l. this site supports the largest, densest stand of *P. hookeri* on the island. At Stony Creek valley, *P. hookeri* grows in a one metre deep aeolian sand deposit atop a peat band that has been dated to 1530 (± 30) y.o., which is superimposed on a thick, much older sand body (Selkirk and Saffigna 1999).

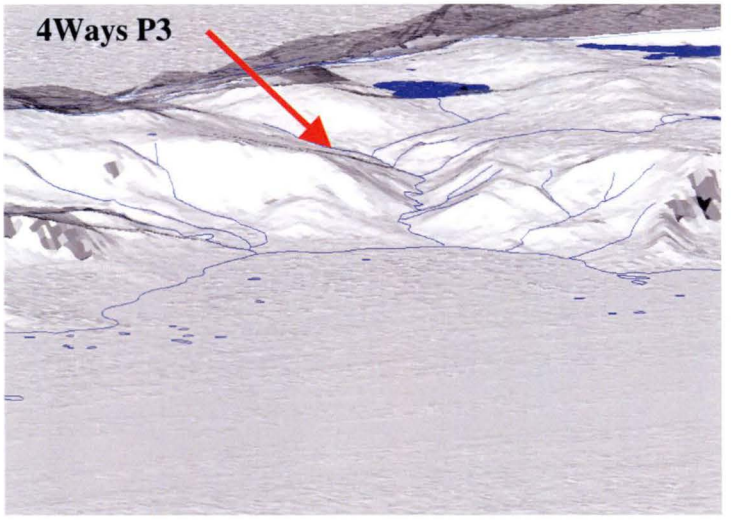


Plate 3.10 P3 on the 4Ways track looking south-east from above Bauer Bay, with Square Lake in the background (SE)

This study also included two lowland sites. The first (P2) was in Green Gorge Basin in *P. hookeri* dominated herbfield at 20 m a. s. l. on the flat area adjacent to a lake. This site is protected as it is exposed mainly to the east. P2 was an oceanic inlet approximately 8 500 years ago and since then has been uplifted as a result of tectonic processes (Bergstrom 1986b).

The other lowland site (P1) was at Handspike Corner on a raised marine terrace, formed from an old wave-cut platform and uplift. Situated at the north-western corner of the island, the site is 1 km wide and up to 15 m a.s.l. The large flat area was predominantly covered with herbfield (*P. hookeri/Coprosma perpusilla*) however, there is a subtle gradation from short grassland to mire to herbfield depending on the drainage patterns of the underlying peat (Taylor 1955; Rich 1996; Selkirk et al 1990b) This terrace represents some of the youngest land on the island (Selkirk et al. 1990a).

There is much temporal and spatial variation of rabbit grazing across the island. At P3 in the early in 1970s all *P. hookeri* rosettes were reduced to grazed stumps at ground level (pers. comm. R Seppelt, N. Brothers, G. Copson). During the study P1 was subject to low grazing intensity probably because it was waterlogged and therefore not suitable for supporting large burrow networks. During the study P2 was subject to regular, light rabbit grazing, whilst P7 was heavily grazed.

Field collections

Five random *S. polaris* plants were harvested at each site once only, as this species flowers annually. Plants were harvested in early autumn during the annual island resupply visit in March, 2002. All living above ground matter was collected, while

below ground only living rhizomes were collected.. At S2 and S3, *S. polaris* has extensive rhizomatous networks with many rhizomes growing amongst and on top each other. It is difficult to harvest without negatively impacting on the surrounding herbfield, therefore, a maximum length of 40 cm of rhizome was collected as several large plants at these sites did have rhizomes that terminated at around 40 cm length. Lateral roots proved difficult to harvest as they were fine (< 1 m in diameter) and interwoven and as a result snapped off, therefore they were omitted from the study. A similar study (Nicholls and Rapson 1999) investigating megaherb biomass had the same difficult harvesting roots, therefore roots were also omitted from their study. Similarly, the below ground tissue harvested were rhizomes.

Five random *P. hookeri* plants were harvested at each site on each of two occasions; once in a flowering year and once in a non-flowering year. Plants were collected at peak leaf expansion in late January to early February 2000, depending on the site. All living above ground matter was collected. Rhizomes grow downward with minimal branching and consequently they were excavated in entirety. The length of each rhizome was measured and the conditions of the terminal ends were defined as: rotten or healthy. As with *S. polaris,* adventitious roots proved difficult to harvest and were omitted from the study.

Another five plants per site were harvested the following summer (2000/2001) and only individuals that had flowered the previous season were collected. The presence of withered racemes attached to the rosette was taken as an indication of flowering.

Harvested plants of both species were sub-divided into various tissue categories, leaf lamina, inflorescence, and for *S. polaris* petiole, as there is no true petiole for *P. hookeri.* All material was then oven dried at 40^0 C. Once dried, the inflorescences were further sub-divided into fruit/flowers, pedicel, peduncle, and capitula. Each component was then weighed.

Data on total plant mass and each tissue mass were analysed with a repeated measures analysis of variance using general linear model procedures in the SAS statistical package, v.8 (SAS Institute Inc. 1988) Significant effects were analysed with a Ryan-Einot-Gabriel-Welsch *post hoc* comparison (Day & Quinn 1989).

Results

Megaherb allocation

Megaherbs produced substantial amounts of biomass with the largest *S. polaris* plant weighing 488g (total dry weight) and *P. hookeri,* 385g (total dry weight). The range in mean total plant biomass was similar with the smallest S. *polaris* being 59 g and for *P. hookeri* 16 g. Both species produced rhizomes and leaves, however, *P. hookeri* only produced flowers once every two years during the study while *S. polaris* flowered every year. When flowering *P. hookeri* allocated a greater proportion of total biomass to sexual reproduction than did *S. polaris* (see Table 3.1)

Large scale site variation

Megaherbs plant biomass varied significantly between sites for both species (see Table 3.1). *Stilbocarpa polaris* plants at S6 (200 m a.s.l) were significantly smaller than those at the two low altitude sites S2 and S3 (20 and 15 m a.s.l. respectively).

The largest plant recorded was found at S3, where *S. polaris* was tall and dominant, forming a thick, dense canopy, however mean plant biomass at S3 was not significantly larger than that from S2. Plants at S6 were significantly smaller ($P<0.001$, $F = 65.2$).

There was a significant site effect on *P. hookeri* biomass ($P<0.001$, $F = 70.3$). The high altitude P7 (370 m a.s.l).and the low altitude P1 (15 m a.s.l) had similarly sized, small plants while the mid altitude P3 (190 m a.s.l.) and low altitude P2 (20 m a.s.l) both supported large plants (Table 3.1). The largest plant was recorded at P3 where *P. hookeri* was its tallest and dominated the herbfield, forming a thick dense canopy.

Tissue allocation

All megaherbs in the study allocated roughly half or more of their total plant biomass to leaf tissue as shown in Table 3.1. All plants allocated the same proportion of total biomass to reproductive tissue. Overall *S. polaris* allocated slightly more tissue to rhizome than reproductive tissue.

Unlike *S. polaris*, flowering *P. hookeri* plants allocated more biomass to reproductive than rhizome tissue, except at P1. In non-flowering years *P. hookeri* leaf and rhizome tissue allocation increased, with most resources going to leaf tissue (up to 80% of total plant biomass). Figure 3.2 shows how both species partition vegetative tissue, (rhizome and leaf tissue, excluding reproductive tissue) and the variation between sites for each species.

Table 3.1. Mean tissue allocation as % of total plant biomass. Within a species and sampling year, those site means with the same letter were not significantly different (P>0.05). Root material was not included due to harvesting difficulties across all sites.

	Site	Mean plant weight (g)	Proportion of plant dry mass (%)		
Pleurophyllum hookeri			**Leaf**	**Rhizome**	**Reproductive**
Flowering year	P1 (15m a. s. l)	49 **b**	54 **a**	28 **a**	18 **b**
	P2 (15m a. s. l)	155 **a**	40 **a**	17 **b**	42 **a**
	P3 (190m a. s. l)	240 **a**	54 **a**	15 **b**	31 **ab**
	P7 (390m a. s l)	37 **b**	50 **a**	17 **b**	32 **ab**
Non flowering year	P1 (15m a. s. l)	35 **b**	56 **b**	43 **a**	0
	P2 (15m a. s. l)	96 **a**	80 **a**	20 **b**	0
	P3 (190m a. s. l)	165 **a**	73 **a**	27 **b**	0
	P7 (390m a s .l)	23 **b**	73 **a**	27 **b**	0
Stilbocarpa polaris	S3 (15m a s. l)	312 **a**	59 **a**	28 **a**	16 **a**
	S2 (20m a. s. l)	404 **a**	47 **a**	33 **a**	20 **a**
	S6 (200m a s l)	86 **b**	65 **b**	16 **b**	19 **a**

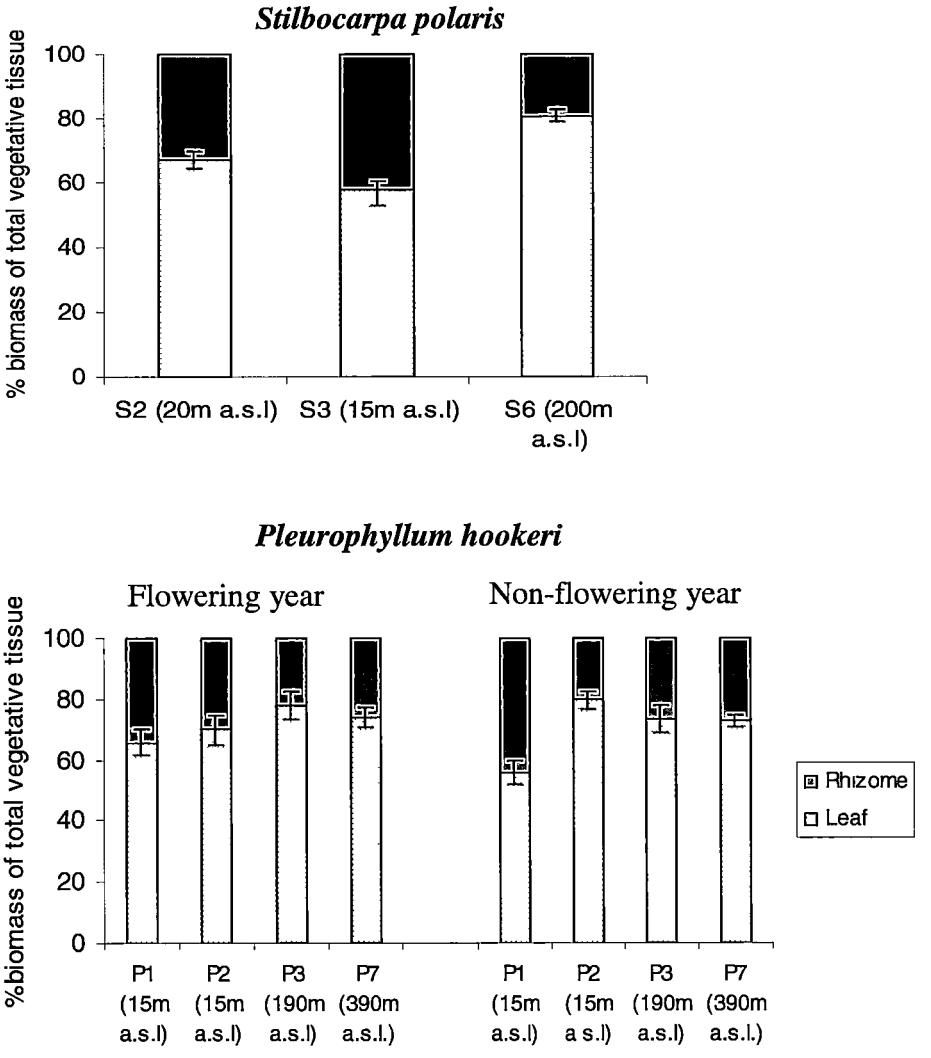


Figure 3.2 Biomass allocation of *S. polaris* (2002) and *P. hookeri* (2000 & 2001) leaf tissue (comprising petiole and lamina) and rhizome tissue as a proportion of vegetative biomass (ie. excluding reproductive tissues).

At the higher altitude site (S6), *S. polaris* allocated a smaller proportion of their total biomass to rhizome tissue than *S. polaris* at other sites. At the low altitude site (P1), *P. hookeri* allocated a greater proportion of total biomass to rhizome tissue than *P. hookeri* at other sites. *P. hookeri* rhizomes varied in length between sites. From the shoot base to the end of the rhizome, the mean lengths per site were; 10.5 $^{\pm}$0.7 cm, 11.1 $^{\pm}$1.4 cm, 22.5 $^{\pm}$2.6 cm, and 7 $^{\pm}$0.8 cm respectively for P1, P2, P3 and P7.

All *S. polaris* plants had the same proportion of biomass (16 - 20%) allocated to reproductive tissue (see Table 3.1). In flowering *P. hookeri* plants there was between site variation in the proportion of reproductive biomass allocated. *P. hookeri* plants at P2 had 42% of total plant biomass allocated to reproductive tissue which was significantly higher than plants at P1 which allocated only 18% of total biomass to reproduction ($P<0.001$).

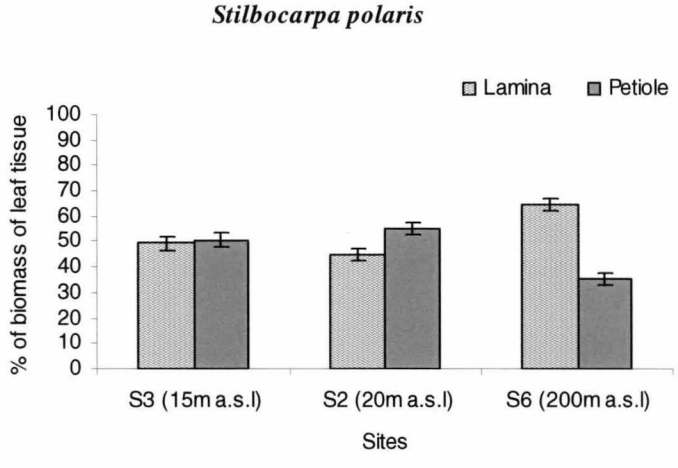


Figure 3.3 Biomass allocation within leaf material for *S. polaris* across all sites, where shaded represents lamina, and grey represents petiole

Micro variation

Despite producing similar amounts of leaf tissue, structural partitioning of the leaf was different for each species. *S. polaris* had laminas subtended on the end of a long petiole while *P. hookeri* petioles were rather indistinguishable from the lamina. Resource allocation within *S. polaris* leaf tissue (lamina and petiole) varied between sites (Figure 3.3). Plants at S3 and S2 allocated the same proportion of biomass to their lamina. Plants at S6 allocated a greater proportion of biomass to leaf tissue as they had reduced petioles, yet plants at S2 allocated significantly more biomass to their petiole than did plants at S6 ($P<0.001$).

Similar to vegetative tissue, reproductive tissue can also be further divided into structural components. Both species produced many inflorescences which are subtended on pedicels, with each *S. polaris* inflorescence having a distinguishable peduncle. Table 3.1 indicated that flowering *S. polaris* plants allocated less total plant biomass to reproductive tissue than flowering *P. hookeri* plants. However this data is not directly comparable as *P. hookeri* does not flower annually, therefore if comparison is made of proportionate biomass allocation over a two year period for *P. hookeri* allocation is more similar with all plants allocating between 55-63% to leaf tissue, 19-35% to rhizome and 10-21% to reproductive tissue, which is quite similar to the values given for *S. polaris* in Table 3.1. However, in figure 3.4 the break down of reproductive tissue into the various structures indicates that *S. polaris* allocated more to fruit, while *P. hookeri* allocated a greater proportion to pedicels.

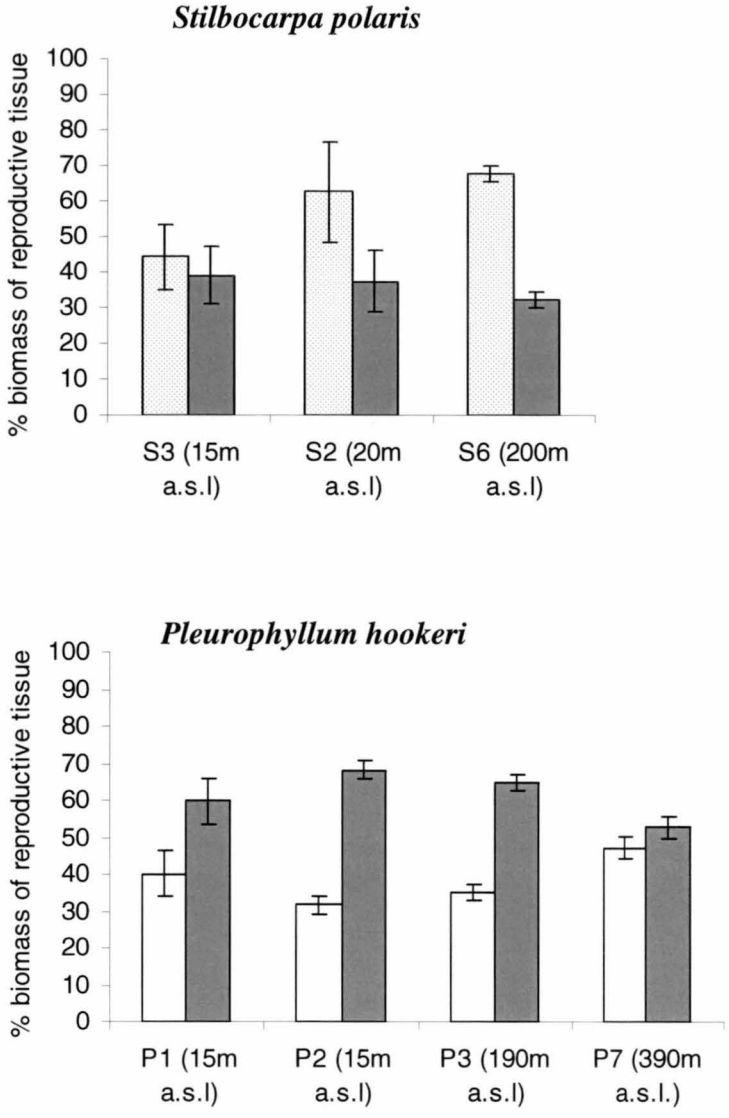


Figure 3.4. Biomass allocated within reproductive tissues for *S .polaris* and *P. hookeri*. Stippled columns represent fruit, and filled columns represent pedicel and peduncle.

Figure 3.5 quantifies the amount of fruit biomass that both megaherbs produced and highlights that it varied with site for both species. *S. polaris* plants produced over 40 g of fruit per plant at S3, while the most fruit produced for *P. hookeri* plants was less than 30 g. High altitude *P. hookeri* plants produced the least amount of pedicel relative to fruit. Overall plants at sites which produced the most leaf tissue (S3, S2, P2, P3) also produced the most fruit.

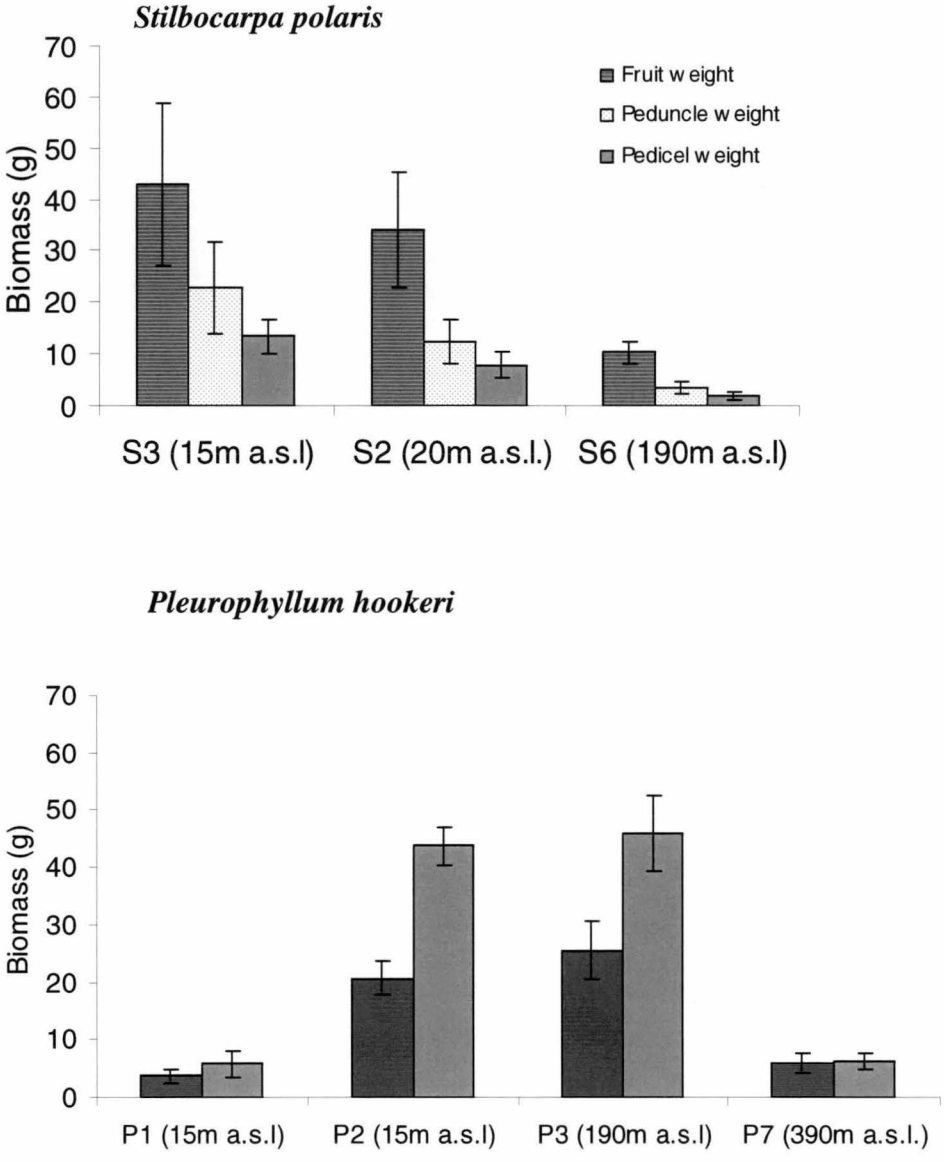


Figure 3.5 Mass (g) of reproductive structures for *P. hookeri* and *S. polaris*. For Grey columns are pedicle weights, hatched columns are fruit weights. *P. hookeri* has no distinguishable peduncles.

Discussion

Megaherbs have been examined by several researchers across the subantarctic (Chapius et al.1994, Jenkin and Ashton 1979; Meurck 1982; Meurck et al.1994; Mitchell et al. 1999; Nichols et al.1999; Scott 1995; Tweedie 2000). Unlike tropical giant rosette forming species of Africa and South America which reach heights of more than 3 m, subantarctic megaherbs only grow up to 1.8 m high. All subantarctic megaherbs show a high leaf:stem ratio relative to other herbaceous plants. Körner (1994) defined the mean leaf mass ratio of a leafy herbaceous perennial as 21% compared to <5% in trees. South American giant rosette forming *Espeletia* allocates an average of 26% of dry matter (including below ground tissue) to leaf biomass (Monasterio 1986). Both of the megaherb species in this study allocated a greater percentage of their biomass to leaves than *Espeletia* sp. *Stilbocarpa polaris* and *Pleurophyllum hookeri* both allocated approximately 50% of biomass to their leaves, which is similar to megaherbs on neighbouring Campbell I. *Pleurophyllum speciosum* from Campbell I. has a leaf mass ratio of approximately 50%, and female *Anisotome latifolia* plants have a leaf mass ratio of between 65 and 70% (calculated from Nicholls and Rapson 1999 including below ground rhizomes). *S. polaris* and *P. hookeri* produced a large below-ground rhizome, which, in this study, contributed approximately 20-30% of total plant biomass. When flowering, megaherbs produced vast numbers of flowers, which accounted for 15-30% of total plant biomass.

This study, along with that of Nicholls and Rapson (1999), shows that functional differences exist between two megaherb species growing in the same island environment. *S. polaris* performs similarly to *Anisotome latifolia* and *P. hookeri* is similar to the congeneric *P. speciosum. S. polaris* invests biomass in long petioles

enabling leaves to maximise light interception, which is similar to *A. latifolia*, and thus creates a canopy. Long petioles display large leaves over a greater surface area of plant than would be possible with short petioles. Alternatively, like *P. speciosum, P. hookeri* has reduced petioles and forms large wide rosettes (up to 75cm wide). This habit also enables the species to shade small neighbouring plants.

Nicholls and Rapson (1999) found that the semi-deciduous species (*P. speciosum*) allocated more biomass to its rhizome which acted as a storage organ while the over-wintering species (*A. latifolia*) allocated more biomass to its leaves. This differs from the Macquarie I. situation, where both *P. hookeri* and *S. polaris* invested similarly in leaf biomass. *P. hookeri* is semi- deciduous shedding most of its leaves in late autumn. *S. polaris* over-winters, however, it undergoes extensive expansion which commences in late spring to early summer (Tweedie 2000). This rapid springtime leaf expansion in both species would require the rhizome to act as a storage organ as results suggest.

The species differed in their reproductive investments, with *P. hookeri* allocating more resources to pedicels than *S. polaris*. The tall pedicels of *P. hookeri* reduce the likelihood of seeds being deposited directly into the centre of the rosette to then become covered with senescing leaves in autumn. *S. polaris* fruits are heavier than those of *P. hookeri* so while initial observations indicate that *S. polaris* produces more fruit, in terms of biomass (g) it is merely that this species produces heavier fruits. Initial counts of inflorescences indicated that both produce similar amounts of seed per individual.

There were sites differences for both species, with high altitude S6 plants being different to those at the other two low altitude sites. The leaf (lamina):petiole ratio decreased at site S6 (200m), where the surrounding vegetation is short herbfield dominated by *Luzula crinita*, *Agrostis magellanica,* and *Acaena magellanica,* all of which are low in stature (<20cm) and do not pose a competitive threat for light and space. At S2, plants compete with *Poa foliosa*, and at S3 there is much intraspecific competition as plants are densely spaced with no bare ground visible. It is difficult to determine if lower competition at S6 has resulted in *S. polaris* being lower in stature, with reduced petioles. The low stature of the vegetation at S6 may be attributed to environmental variance from lower sites (i.e. approximately 190 m difference in altitude) and therefore lower plant productivity (Tweedie 2000). However, the exact determinates of *S. polaris* leaf growth are unknown, the role of wind, light, stored reserves, and nutrient availablity has not been quanitified. The grazing history of the site may influence the community structure. Future studies should monitor the *S. polaris* plants at this site to determine if they have the ability to grow taller in conjunction with the surrounding vegetation which is likely to occur if grazing pressure stays low (Scott 1996).

Interestingly plants, at the high altitude site (S6) have the lowest allocation to the rhizome. Scott (1995) found that high altitude *S. polaris* plants (140 –165 m a.s.l.) had a lower incidence of leaf senescence during winter months than those at lower altitudes. This retention of leaves may reduce the storage requirement of the rhizome as there are existing functioning leaves at the commencement of spring. Therefore *S. polaris* may not require the same rhizome investment in this habitat as these leaves would be photosynthesising. One of the obvious limitations of this study is the

difficulty in quantifying rhizomatous tissue of *S. polaris* at the low altitude sites. Once rhizomes were over 40 cm long they often supported several shoots. In future, if such shoots could be measured in a non-destructive method, more could be ascertained regarding shoot-rhizome relationships and seasonal source:sink patterns.

As much as 20% of the potential seasonal photosynthetic carbon gain may be sacrificed through self shading by plants during flower display (Körner 1999). *P. hookeri* plants overcome this limitation by flowering only once every two years. The most expensive structure for flowering, in lowland forbs, often is the flowering stalk (peduncle); an organ that is drastically reduced at high elevation (Körner & Renhardt 1987, Bauert 1993 both in Körner 1999). This was true for *P. hookeri,* in which, pedicel biomass was smallest (16.5 % of total mass) at the site of highest altitude (P7). Figure 3.4 shows that *S. polaris* pedicels are also reduced in size at the high altitude site (S3). It is expected that pedicel height would be resultant of plant biomass and consequently greatly influencing plant dispersal. In herbfields containing tall plants, tall pedicels are advantageous as most pedicels simply fall to the ground thus ensuring that fruit are not dispersed onto the adult foliage. Some *S. polaris* inflorescences are wind dispersed (ie rolled by the wind) tall pedicels would assist this dispersal process as inflorescences are not dispersed directly beneath the protective canopy. Pedicels of both species were green and therefore presumably photosynthetic increasing the photosynthetic potential of the plants.

Nicholls and Rapson (1999) give total plant dry weights (rhizome, stem, reproductive and foliage tissue) as 220g for *Pleurophyllum speciosum* and 180g *Anisotome latifolia* at 140m a.s.l. on Campbell I. The total plant biomass of *P. hookeri* plants growing at a

higher elevation (P3) in a colder environment (Macquarie I.) is greater than that given for *P. speciosum.* At low altitudes *S. polaris* was considerably more productive than both Campbell I megaherb species. Jenkin and Ashton (1970) found that above ground mass of *P. hookeri* decreased with increasing altitude (0.76 kg m^{-2} at low altitude sites and 0.47 kg m^{-2} for mid altitude site). Tweedie (2000) measured an increase in shoot density and an almost linear decrease in plant height with increasing altitude for *S. polaris.* However, Scott (1995) found that no simple relationship existed between growth rate and overall size of *S. polaris* plants and any single environmental factor. It is important to note that these three studies (Jenkin and Scott 1970; Scott 1995; Tweedie 2000) have used different expressions for plant growth therefore making comparisons difficult.

The current study supports the findings of Scott (1984). It is widely accepted that a strong relationship between altitude and plant performance exists. However, this study shows that modelling plant performance on altitude alone can be misleading. Despite *S. polaris* plants at low altitude being similar, altitude alone was not the only determinant of *P. hookeri* performance. P1 and P7 straddle an altitude gradient of approximately 370 m yet they are most similar in terms of plant biomass (see Table 3.1 and Figure 3.2). Plants at P1 allocate more biomass into rhizome tissue than at any other site, which is typical of plants grown in low nutrient environments (Fitter 1997).

Handspike Corner (P1) supports water logged mire communities on low nutrient soils. In a previous study examining the patterned mires of the Handspike area, Rich (1996) looked at *P. hookeri* distribution. Rich (1996) stated the contractile stems which maintains plants at the mire surface, and vertical stem growth allows them to keep

pace with mire accretion making them suited to the waterlogged environment of a mire. Comparisons of *P. hookeri* root morphology between the blanket and patterned mires were similar. Like the current study, all rhizomes were decayed at the terminal end. However, the rhizome depths given (35 cm) were greater than those observed in this study (20 cm). Rich found *P. hookeri* colonised the drier areas (ridge tops) within a patterned a mire where surface water drainage is possible.

P. hookeri plants were biggest, and had the longest rhizomes at P3. The study has shown that conditions at the site are the most conducive for growth and productivity of all sites measured. The beach sand, which has been deposited at the site (Selkirk and Saffigna 1999) creates free-draining soils. This means the terminal end of the rhizome is not in contact with water table and therefore decays less rapidly than at waterlogged sites. However, it is not only soil structure or consequent waterlogging that determines rhizome length. Plants growing at P7 were growing in mineral feldmark soils, which are free draining. The very short rhizomes measured on plants at P7 are probably resultant of slow plant growth due to low temperatures and low nutrient availability. At P3 both aeolian and fluvial processes operate (Selkirk and Saffigna 1999). Sand is regularly deposited by westerly winds and removed by water, *P. hookeri* plants collect sand but can also become exposed as sand is removed. Selkirk and Saffigna (1999) suggested that *P. hookeri* pedestal's upward growth rate was equivalent to the rate of sand accumulation, which may also account for the long rhizomes measured at the site. Again this study highlights the complex interactions between soil structure, waterlogging, nutrients, and climate that govern productivity in *P. hookeri.*

Interestingly, P3 is the first location on the island where the biological control agent *Myxomatosis cuniculi* (myxoma virus) was introduced to the island's rabbit population in the summer of 1978/79. Prior to this the site was heavily grazed, with rosettes regularly grazed to ground level (pers. comm. N. Brothers, G. Copson, R. Seppelt). It is possible that the large, high stature of *P. hookeri* at the site may be due to length of time since grazing pressure was reduced. However grazing pressure is not consistent across the island and other sites in this study are unlikely to have ever been exposed to intense grazing, and yet they produce smaller *P. hookeri* plants.

There are obvious limitations to this study. Tweedie (2000) and Jenkin (1972) proposed that harvest estimates of biomass can be misleading as species attain their maximum biomass at different times. As shown in this study there can also be intraspecific variation across of a range of environments. This study attempted to overcome these hurdles by harvesting both species during maximum expansion in late autumn and measuring plants across range of sites. At time of harvesting all *P. hookeri* plants had ripe fruits and leaves were about to commence senescence. Some *S. polaris* fruits at S6 were not yet fully ripe, and therefore, there may have been lighter ripe fruits at other sites, however, there was no significant difference between sites and fruit weight/ plant.

The macrophyllous, megaherb growth form has evolved independently in number of diverse plant families in the subantarctic (Mitchell et al. 1999). These authors suggested it is the balance of available water and nutrients, constant temperature and absence of grazing mammals that lead to the evolution of the megaherb form. Perhaps the ability to produce large amounts of photosynthetic leaf material, as measured in

this study, enables megaherbs to overcome low light, wind damage and create a microclimate around the plant, enabling them to be widespread and successful across the subantarctic.

Importantly, both species allocated a substantial proportion of their biomass to sexual reproduction, indicating that seed production is likely to be an important aspect of the biology of these dominant subantarctic species.

Chapter 4 – Megaherb seedling emergence and population recruitment

Introduction

Megaherbs invest heavily in sexual reproduction (Chapter 3) yet little is known of seed fate. This study investigated seedling emergence and seedling survival and how they might influence megaherb recruitment. Sexual reproduction is generally reduced when plants approach the physiological limit of their range (Billings and Mooney 1968; Bliss 1971; Körner 1999; Tweedie 2000). Investigating recruitment processes in plants is fundamental for understanding plant population dynamics (Eriksson and Erhlen 1992). Seeds have the ability to disperse and therefore expand the range of populations and seedling establishment is a critical step for population regeneration (Silvertown and Lovett Doust 1993; Clarke and Davison 2004). In many plant life cycles the seedling stage is the most sensitive (Shimono and Kudo 2003).

Stilbocarpa polaris and *Pleurophyllum hookeri* form a major part of Macquarie I. vegetation, being both abundant and widespread (Copson 1984). Adult *S. polaris* plants bear one to four inflorescences each year, although this varies from site to site (Chapter 3). Inflorescences can bear up to 10 400 individual fruits, each containing 2-4 seeds, which can equate to a single plant producing over 40 000 seeds in a season.

Pleurophyllum hookeri is semi-masting species, which also has a varied flowering effort across sites (Chapter 3). *P. hookeri* racemes can bear up to 23 capitula each

containing up to 100 seeds and therefore one individual plant can produce 43 700 seeds in a season since plants produce up to 19 racemes.

Both species are restricted to Southern Ocean islands and are well adapted to this subantarctic environment, having hairy thick leaves, thick rhizomes for storage, and maximum photosynthesis occurring at low light levels (Jenkin 1972; Tweedie 2000). *P. hookeri* and *S. polaris* have been regarded as clonal plants relying on vegetative expansion via the rhizome (Jenkin and Ashton 1979), although, more recently studies have identified that seedlings can play an important role in subantarctic megaherb regeneration after the removal of grazing feral vertebrates (Meurk 1982; Meurk et al. 1994b; Chapuis et al. 2004).

This study aimed to determine:

- seedling emergence levels in megaherb populations;
- if there are seasonal patterns in seedling emergence;
- levels of seedling mortality;
- which environmental factors may be related to seedling mortality; and
- if these vary among populations

Materials and Methods

Site descriptions

Seedling recruitment was assessed at a range of sites where megaherbs dominated or were co-dominant, with each site being 20 m x 20 m in area. Sites varied in physical attributes, such as soil structure, aspect, exposure, and altitude (see Plate 4.1).

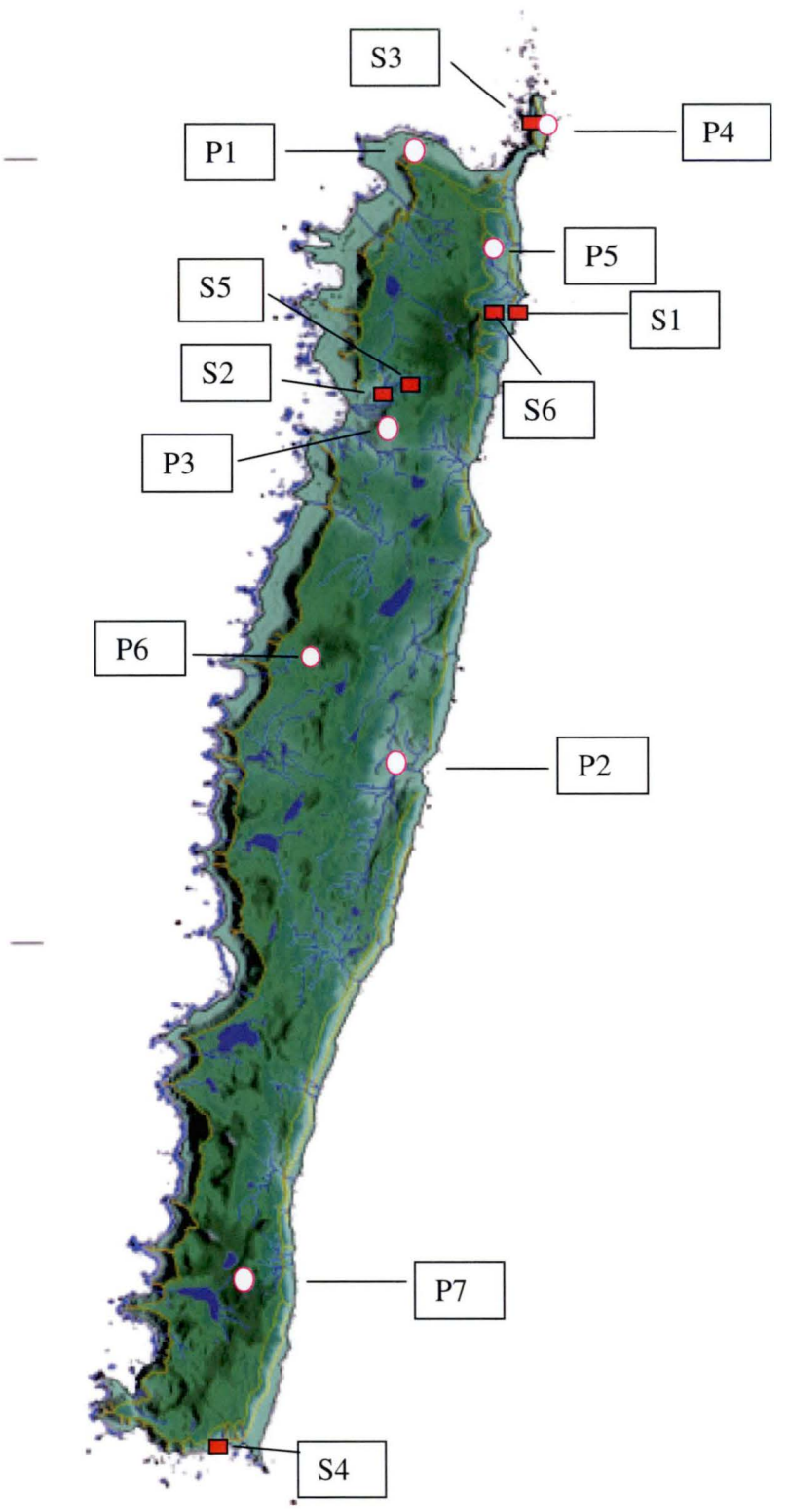


Plate 4.1 . Map of Macquarie I. showing study sites ■ is a *S. polaris* site

○ is a *P. hookeri* site

Seedling plots

Large piles of fruit of both species were visible on the ground amongst adult plants, where ripe inflorescences had fallen during autumn (*P. hookeri*) and early winter (*S. polaris*). Field observations prior to the commencement of the study found seedlings occurred beneath these fallen inflorescences at all sites. At each site, six random seed piles were selected and study plots were installed, i.e. a presence of seeds was selected for, and only where seed piles were >1 cm deep. No measure was made of the number of seeds within each plot. *S. polaris* seed piles were usually derived from one inflorescence while *P. hookeri* seed piles were derived from several inflorescences of one plant. Plots were 20 cm x 20 cm, marked at each corner with small plastic pegs.

Control plots were randomly placed at some sites (see Table 4.1) and were the same dimensions as seedling plots (20 cm x 20 cm) with no seeds visible within each plot. At two *P. hookeri* sites (see Table 4.1) extra seedling plots were installed because seed piles were numerous. At sites P4 and P5 feral rats dispersed seeds, therefore, the six seedling plots were established on animal constructed piles of seeds (rat impacts on seedlings are dealt with separately in Chapter 6).

Table 4.1 Summary of survey methodologies employed at each site. Variations in site surveys are due to logistic constraints of travel time to remote sites. For survey frequency "infrequent" refers to only three or less sampling events during the study.

	Site Summary							
Site	Community composition	Pop. attributes	Number of Seed plots	Number of Control plots	Start of Seedling surveys	Resurvey 2002	Survey frequency	Dispersal mode
Pleurophyllum hookeri								
P1	✓	✓	6		August		Regular	Wind gravity
P2	✓	✓	12		August	✓	Regular	Wind gravity
P3	✓	✓	12	6	July	✓	Regular	Wind gravity
P4	✓	✓	6		June	✓	Regular	Rats
P5	✓		6		June	✓	Regular	Rats
P6			6		November		Infrequent	Wind gravity
P7	✓	✓	6		November		Infrequent	Wind gravity
Stilbocarpa polaris								
S1	✓	✓	6	6	July	✓	Regular	Wind gravity
S2	✓	✓	6	6	August	✓	Regular	Wind gravity
S3	✓	✓	6	6	August	✓	Regular	Wind gravity
S4	✓		6	6	October		Infrequent	Wind gravity
S5	✓	✓	6	6	August		Regular	Wind gravity
S6	✓		6	6	July		Infrequent	

Seedling surveys

The study was initiated in June 2000 and surveying continued through to March 2001, however, survey frequency of each site varied. The total number of seedlings within the plot was counted each visit. Surveys were only performed when the ground was snow–free. Most sites were surveyed every 4 to 7 weeks, but four high altitude sites were subject to infrequent surveying, due to the time taken to travel to these remote

sites (see Table 4.1). Mortality was determined by a decrease in seedling density between sampling periods.

A short visit to the island twelve months later, in March 2002, enabled some opportunistic sampling at three sites. Only some plots within each site were relocated. At this time, mature seedlings, as identified by mature leaves and the absence of cotyledons, provided an indication of seedling survivorship to 12 months (March 2001 to March 2002). At each visit the presence of other species of emergent seedlings was recorded. Canopy cover over the plot was assessed as being open, half-open or closed, and leaf deposition onto the plot was monitored. The presence of rat, mouse and rabbits scats and also slugs within or directly adjacent to plots (<20 cm) was recorded each visit.

Community composition

Species composition at each site was measured within 1 m x1 m quadrats centred on each seedling and control plot, and all vascular species within the quadrat recorded (see Table 4.2). At each site a minimum of twelve quadrats was surveyed, except at one site (P6) where due to logistic constraints, only six quadrats were surveyed. Species cover, bryophyte cover and the amount of bare ground was estimated. Soil moisture was determined by field observations of the amount of surface water and the soil peat content. Vertebrate-induced disturbance at the sites was monitored, with rabbit grazing recorded as number of grazed plants m^{-2} (Plate 4.2 and 4.3).

Plate 4.2. *P. hookeri* rosette grazed by rabbits

Plate 4.3. *S. polaris* plants heavily grazed by rabbits, Rhizomes and above ground tissue have been eaten. *Poa annua*, *Epilobium pedunculare*, *Cardamine corymbosa* are colonizing the area

At several sites automatic weather stations were installed to give an initial indication of microclimate amongst herbfields; however, these instruments were not available for the entire duration of the study therefore climate data is sporadic. One weather station was placed at 10 m a.s.l. at the northern end of the island, amongst *S. polaris* plants to measure microclimatic variation between canopy-covered and gap environments. The weather station logged air temperature, soil temperature, and incoming solar radiation. There were two of each sensor, one placed in a naturally created gap (approximately 1 m x 1 m) the other placed under the *S. polaris* canopy (60 cm high). Solar radiation ($MJ/m^2/sec$) was measured at 35 cm using photoelectric pyranometers each positioned on its own mast. Soil temperature was measured using probes placed in the soils at 5 cm depth. Air temperature was measured using a Viasala sensor at 35 cm above ground . All sensors logged to a 50 channel six-volt DT 500 Datataker datalogger (Data Electronics Australia Pty Ltd). Sensors recorded climatic data from all sensors every two minutes and logged an average of 10 readings every 20 minutes. This regime and equipment was similar to that used by Tweedie (2000).

Population attributes

Stilbocarpa polaris population attributes were estimated at each site using 1 m x 1 m random quadrats and the number of flowering individual *S. polaris* plants was recorded (see Table 4.2 and Plate 4.4). During the study the population at S4 was heavily grazed by rabbits with all standing vegetation removed therefore no population attributes could be collected. Due to logistic complications no measurements could be made at S6. Previously Skotnicki et al. (2003) detected a virus

in the Macquarie I. *S. polaris* population, therefore during this study each population was visually checked for the virus whilst population attributes were measured.

The number of flowering *P. hookeri* plants was recorded at most sites (see Table 4.2) by surveying every plant within a 5 x 5m plot. At P4 only 16 random 1 m x 1 m quadrats were surveyed, and no flowering information was obtained for P5 and P6 due to logistic constraints.

Data on seedling density were analysed with a repeated measures and multiple model analysis of variance using general linear model procedures in the SAS statistical package, v.8 (SAS Institute Inc. 1988) Significant effects were analysed with a Ryan-Einot-Gabriel-Welsch *post hoc* comparison (Day and Quinn 1989).

Plate 4.4 *S. polaris* population attributes surveying at S3 (Aerial Cove) with 1 m x1 m quadrat.

Table 4.2a. Site attributes for *Stilbocarpa polaris* populations. (*na* indicates no information was available or collected)

Sites	**S1**	**S2**	**S3**	**S4**	**S5**	**S6**
Location	Mt Elder (10m site)	Bauer Creek Lower	Aerial Cove	Hurd Point	Bauer Creek Upper	Mt Elder (200m site)
Altitude	10m	20m	20m	20m	50m	190m
Vegetation type	Herbfield / TTG	Herbfield/ TTG	Herbfield/ TTG	Herbfield/ TTG	Herbfield	Herbfield
Aspect	East	West	North West	South East	West	East
Moisture scale	Moist	Wet-saturated	Moist	Moist-dry	Moist-dry	Moist-dry
rabbit grazed plots ($1m^2$)	58%	8%	0	100%	42%	0
# vascular plant species	12	10	5	7	15	na
Bryophyte cover	10%	0-10%	10-20%	20%	10-20%	na
Bare ground	0%	20%	20%	10-20%	30-40%	na
S. polaris inflorescences m^{-2}	2.8 ± 0.4	2.0 ± 0.5	4.6 ± 0.9	0	0.9 ± 0.4	na

Table 4.2b. Site attributes for *Pleurophyllum hookeri* populations (*na* indicates no information was available or collected)

Sites	**P1**	**P2**	**P3**	**P4**	**P5**	**P6**	**P7**
Location	Handspike Point	Green Gorge Basin	4 Ways	Lambing Gully	Gadgets Gully	Mt Eitel	Windy
Altitude	15m	15m	190m	80m	210m	280m	350m
Vegetation type	Mire-herbfield	Herbfield	Herbfield	Herbfield	Herbfield	Feldmark	Feldmark
Aspect	West	East	South west	North east	East	South	North west
Moisture scale	Wet	Wet	Moist-dry	Wet	Moist	Dry	Dry
Rabbit grazed plants (m^{-2})	0	2.2%	11%	0	0	75%	91%
# vascular plant species	12	9	7	12	7	10	6
Bryophyte cover	10%	25%	<10%	10%	25%	20%	<10%
Bare ground	0%	10%	0%	0%	0%	55%	0%
Flowering *P. hookeri* plants m^{-2}	$4^{\pm 1.9}$	$2.9^{\pm 1.7}$	$6.3^{\pm 1.5}$	$7.1^{\pm 0.5}$	na	na	$1.9^{\pm 1.4}$

Results

Seedlings of megaherbs, *P. hookeri* or *S. polaris*, emerged at all sites investigated. Where there was a deposition of megaherb seeds there was a 98% likelihood of megaherb seedlings emerging. Only two seed plots showed no germination throughout the entire study one plot at each of the high altitude *P. hookeri* sites (P6 and P7). The first seedlings for *P. hookeri* emerged in July and for *S. polaris* in August.

High seedling densities were observed for both species of megaherb with the highest recorded density 10 500 seedlings m^{-2} at P4 in a rat-dispersed *P. hookeri* seed pile. Seed density was still high for naturally dispersed seed with the highest recorded density for *S. polaris* at 2 250 seedlings m^{-2} and for *P. hookeri,* 1 850 seedlings m^{-2}.

Maximum mean seedling density varied between sites and was greater for *P. hookeri* (17 m^{-2} to 1791 m^{-2}) than *S. polaris* (147 m^{-2} to 688 m^{-2}). There were significant differences in seedling density between populations of each species (Table 4.3 and Figure 4.2); however, each species' data was analysed differently. For *P. hookeri* a site x time relationship was found ($P<0.0001$, $F=5.76$) across most sites in several given months (Figure 4.2). However, sampling times of *S. polaris* did not overlap as well for time analysis and therefore, only the mean maximum seedling densities were compared across all sites showing there was a significant site effect on seedling density ($P<0.0001$, $F=5.53$). For both species, the sites with the greatest density of flowering plants (Table 4.2) had the greatest seedling densities (Figure 4.2 P3 and Figure 4.1 S3)

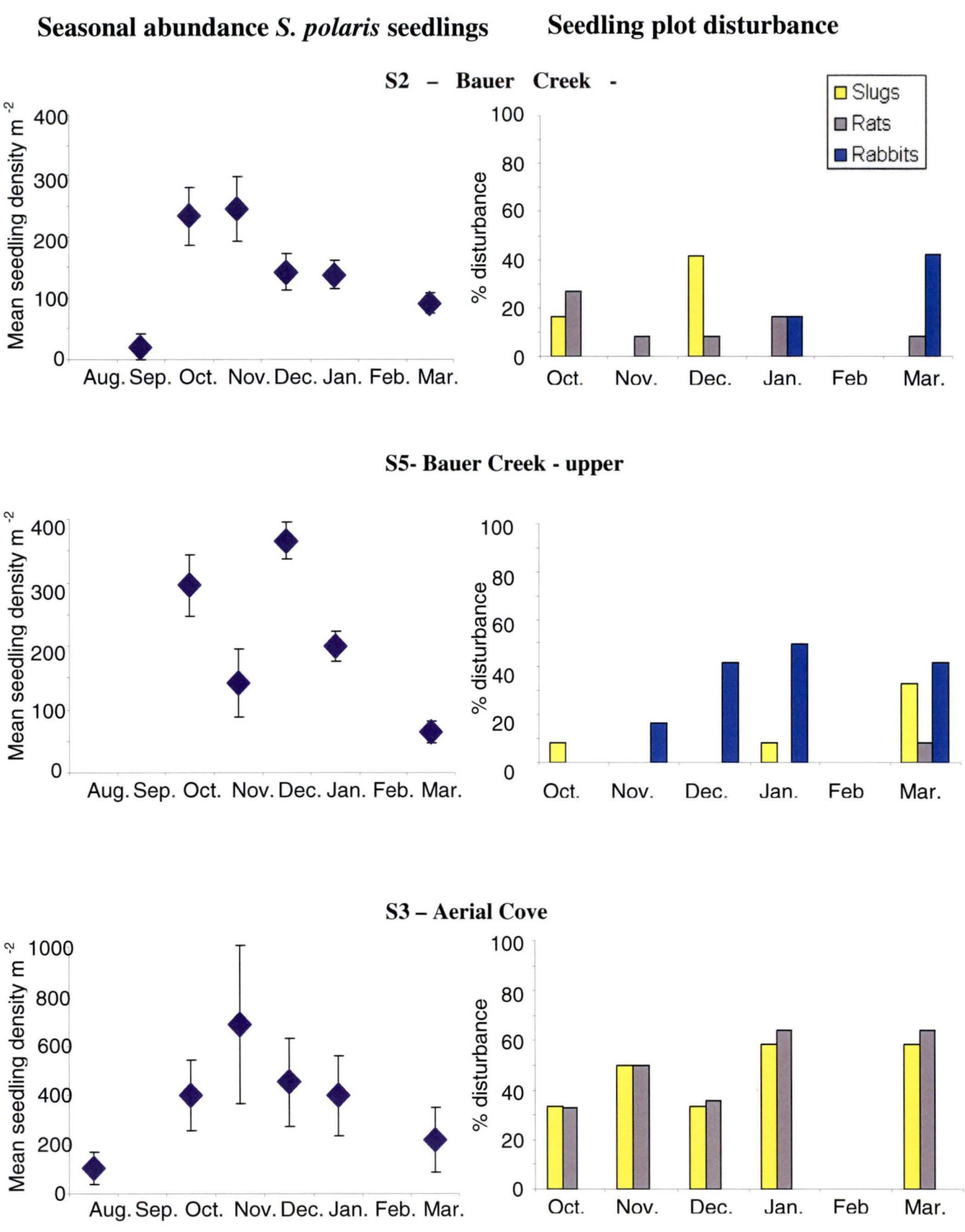


Figure 4.1a Mean *S. polaris* (± s.e.) seedling densities at each site and the proportion of plots disturbed by rats (grey), rabbits (blue) and slugs (yellow).

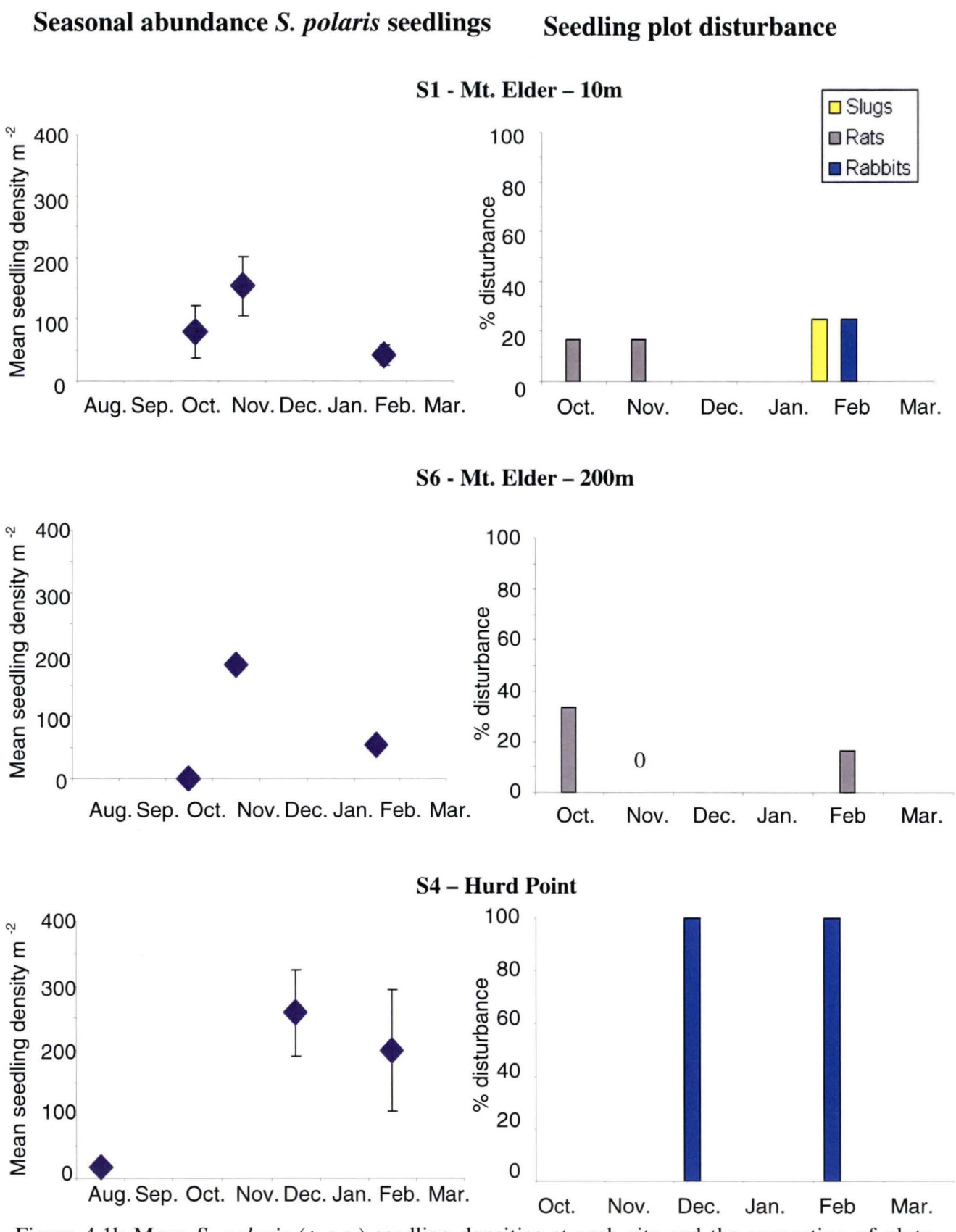


Figure 4.1b Mean *S. polaris* (± s.e.) seedling densities at each site and the proportion of plots disturbed by rats (grey), rabbits (blue) and slugs (yellow). 0 represents sampling event with no value.

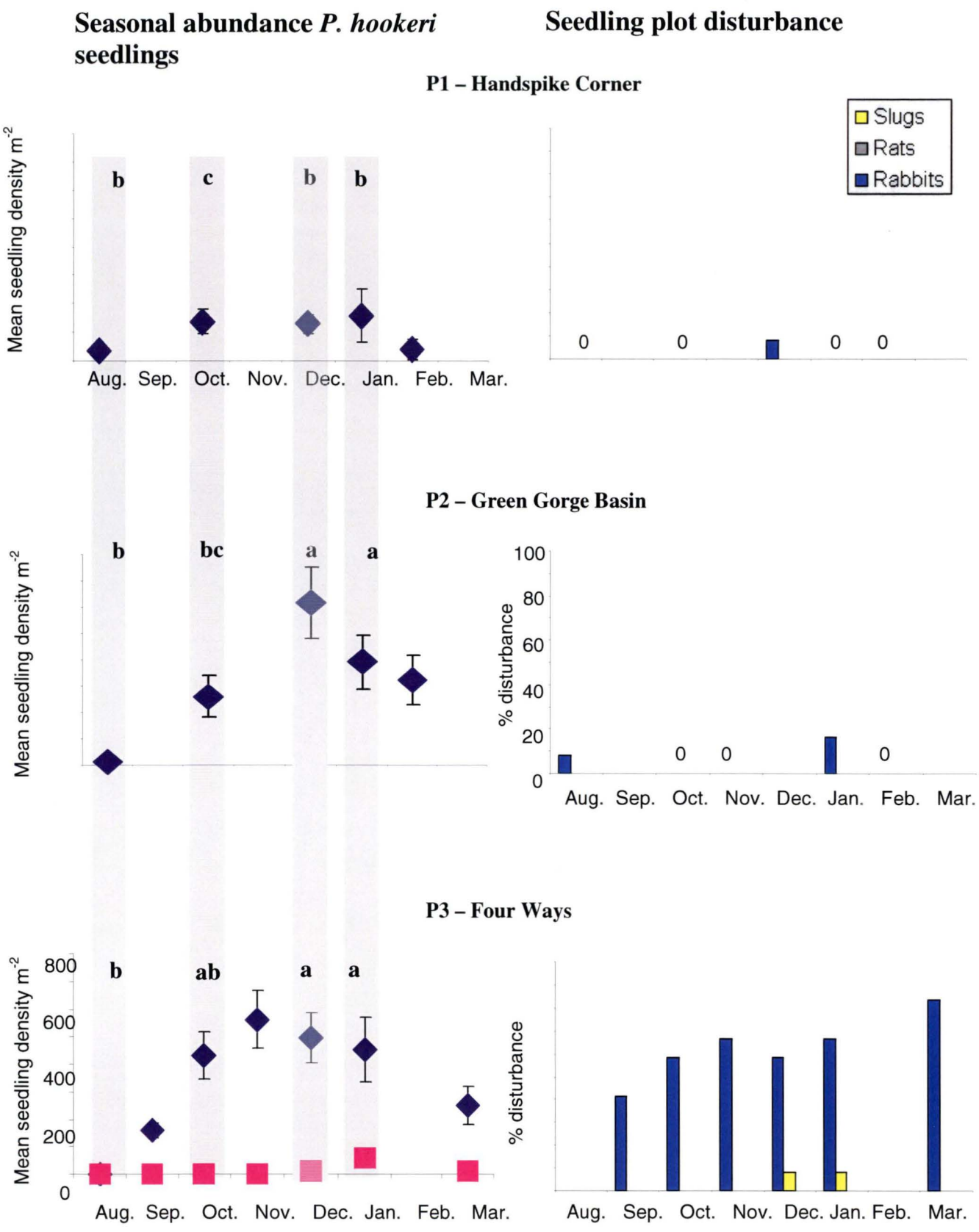


Figure 4.2a Mean *P. hookeri* seedling densities (± s.e.) at each site and the proportion of plots disturbed by rats (grey), rabbits (blue) and slugs (yellow). 0 represents sampling event with no value. Bold letters show significant differences over time, same letters are not significantly different. Pink points represent control plots.

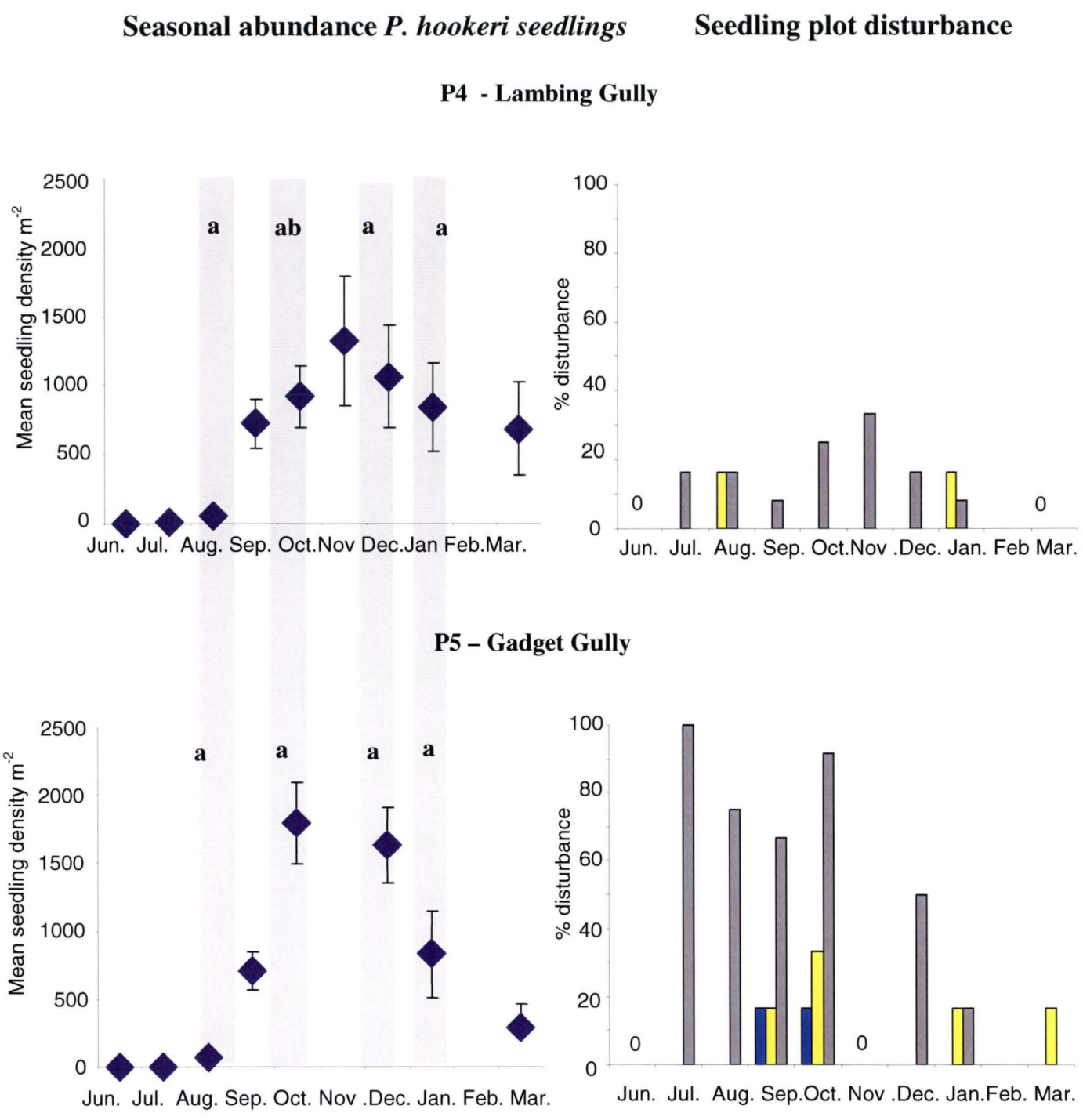


Figure 4.2b Mean *P. hookeri* seedling densities (± s.e.) at each site and the proportion of plots disturbed by rats (grey), rabbits (blue) and slugs (yellow). 0 represents sampling event with no value. Bold letters show significant differences over time, same letters are not significantly different.

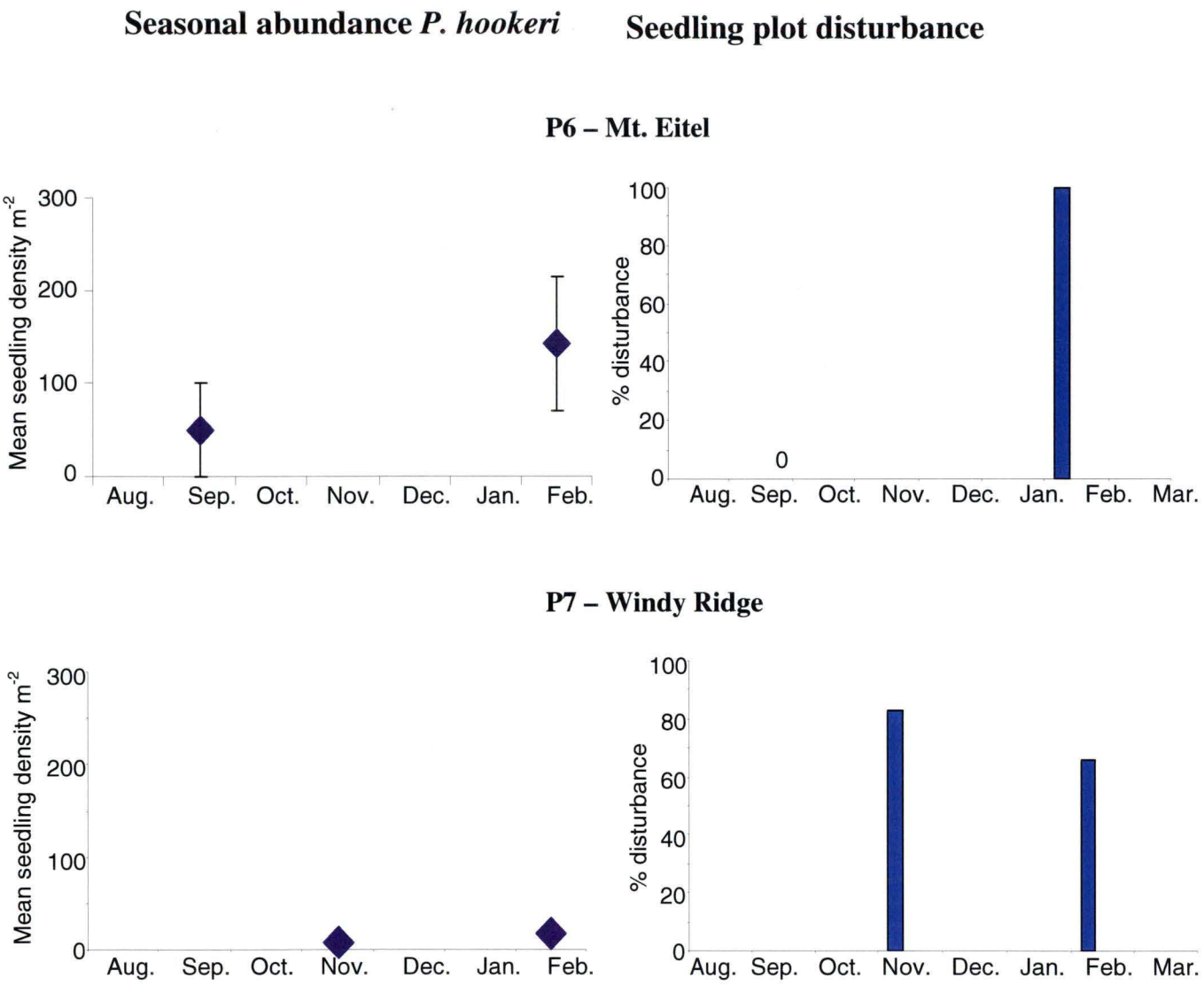


Figure 4.2c Mean *P. hookeri* seedling densities (± s.e.) at each site and the proportion of plots disturbed by rats (grey), rabbits (blue) and slugs (yellow). 0 represents sampling event with no value.

Table 4.3. *Ryan-Einot-Gabriel-Welsch* multiple range test groupings of seedling densities across all *S. polaris* sites during the study, where bold letters indicate site groupings, ie. same letters are not significantly different. Mean seedling density for each site is given.

Stilbocarpa polaris sites	Range of mean seedling density (seedlings m^{-2}) during study	
S1	59.5	**bc**
S2	76.3	**bc**
S3	379.8	**a**
S4	83.8	**b**
S5	123.2	**bc**
S6	45.4	**c**

There was also great variation within populations, which is represented by the high standard errors in Figure 4.1 and 4.2. *Stilbocarpa polaris* had the greatest within-site range of seedling density at any one time, with 0- 2250 seedlings m^{-2} at one site (S3) in November (Figure 4.1), compared to 150- 1850 seedling m^{-2} for *P. hookeri* at one site (P3) in December (Figure 4.2).

Overall, 30% of control plots produced seedlings, although seedling densities were significantly lower ($P<0.0001$, $F=77.04$) for both species, than those of seed plots, with only one or two seedlings emerging in each control plot during the study. The highest seedling density recorded within a control plot was for *P. hookeri* at P3 (200 seedlings m^{-2}) and for *S. polaris* at S2 (100 seedlings m^{-2}). Several of these seedlings survived until mid autumn 2001, however, none survived to autumn 2002.

Altitude alone did not determine emergence time as mid-altitude *P. hookeri* populations germinated first in July. In spring, two low altitude *P. hookeri* sites (P1

and P2) had significantly different seedling densities, while P2 and P3 had similar seedling densities (Figure 4.2) despite their 180m altitude difference.

Across all *P. hookeri* and *S. polaris* sites seedling densities were significantly higher (*P. hookeri* $P<0.0001$, $F= 47.58$; *S. polaris* $P<0.0001$, $F= 3.74$) in late spring and early summer (Figure 4.2). Figures 4.1 and 4.2 show a peak in seedling mortality between mid summer and early autumn. Figure 4.3 shows that end of season (autumn 2001), seedling densities were higher for *P. hookeri* than *S. polaris*, indicating there was greater mortality in *S. polaris* during the first summer.

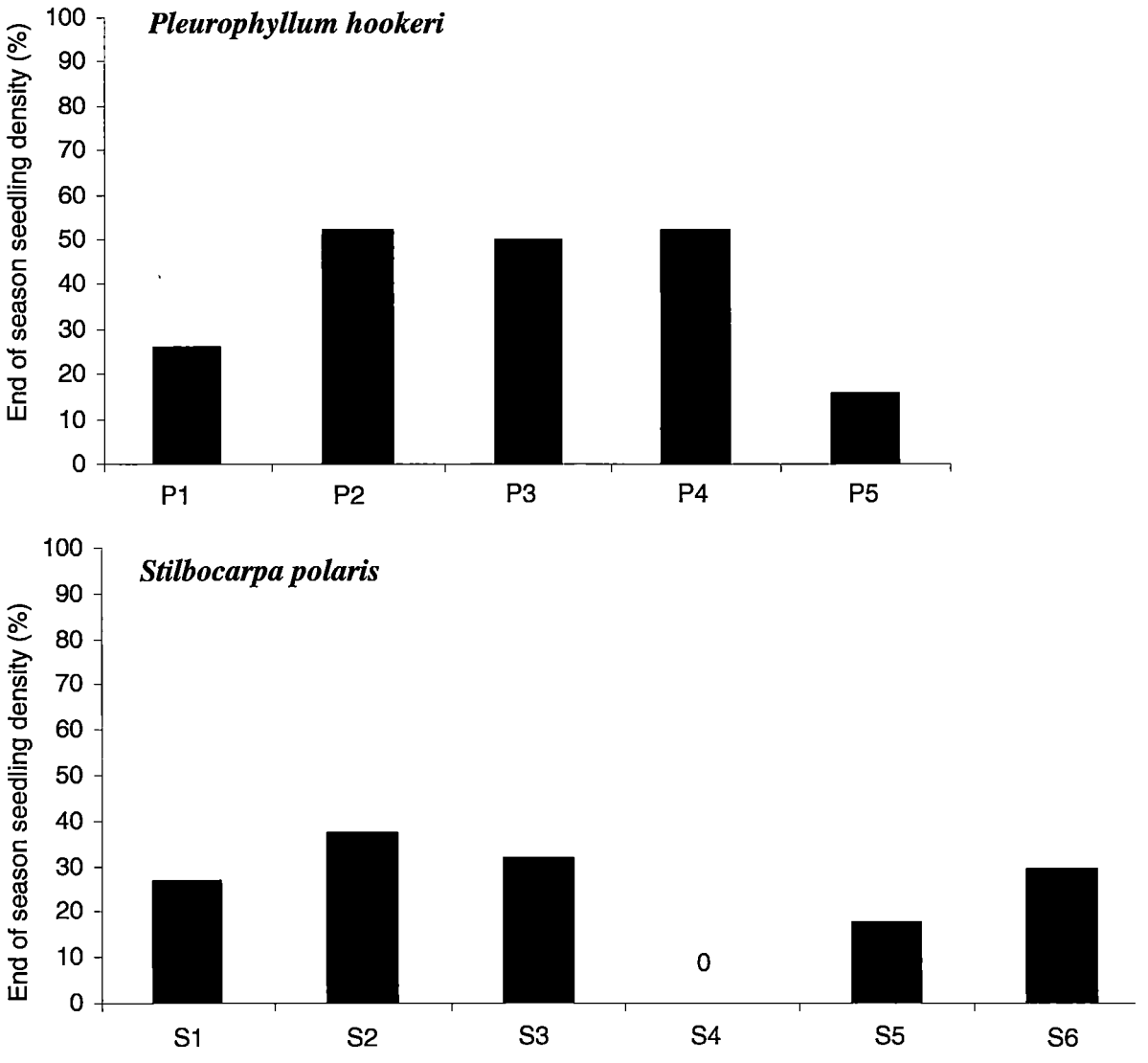


Figure 4.3 Seasonal variations in mean seedling density, where the end of summer seedling density is shown as a proportion of the maximum mean seedling density in mid summer. Note at S4 (Hurd Pt) rabbits had destroyed all seedlings by the end of summer 2001.

Megaherb seedling mortality was high across all sites (Table 4.4a & b). From the period from first emergence to autumn 2001 the number of seedlings decreased dramatically and continued to decrease to the following autumn (2002). Overall 60% of *S. polaris* seedlings died during the 18 month study. At one site (S5) more than 80% of *S. polaris* seedlings died during the first summer. Seedling survival was higher for *P. hookeri* with three sites having > 45% survivorship.

Table 4.4a. *S. polaris* seedling survivorship for each plot resurveyed in March 2002. (Not all plots could be relocated at S3).

	Sites			
Plot number	S1	S2	S3	S6
1	0	0.4	0.6	1.0
2	1.0	0	0.1	0
3	1.0	0	0	1.0
4	0	0	0.27	0
5	0	0	0	-
6	0	0	0	0.5
7	-	-	0	-
8	-	-	0	-
Mean seedling survivorship	0.33 ±0.21	0.06 ±0.06	0.09 ±0.05	0.5 ±0.22
Proportion of plots with 100% mortality	0.66	0.83	0.63	0.5
Total number of survivors at each site	4	2	18	10
Total density of surviving seedlings/m^2	33	50	150	83
Density of NEW seedlings/m^2	100	0	700	475

Table 4.4b. *P. hookeri* seedling survivorship for each plot resurveyed in March 2002. (Not all plots could be relocated at P2.)

	Sites			
Plot number	P2	P3	P4	P5
1	0	0	1.0	0.33
2	-	0	1.0	0
3	0	0	0.1	0
4	0	0	0.27	1.0
5	-	0.05	0	0
6	0.09	0	0.58	0.05
7	0	0	-	-
8	0	0	-	-
9	0.33	0	-	-
10	0.13	0	-	-
11	-	0	-	-
12	-	0	-	-
Mean seedling survivorship	0.07 ±0.04	0.004 ±0.004	0.49 ±0.18	0.23 ±0.16
Proportion of plots with 100% mortality	0.62	0.91	0.16	0.50
Total number of survivors	6	1	65	7
Total density of surviving seedlings/m^2	50	25	325	58
Density of NEW seedlings/m^2	75	0	0	0

Disturbances

Rabbits were present at most sites (Table 4.2a and 4.2b) having a consistent presence at P3 and a strong impact at P7 and S4. Slugs were also present at many *P. hookeri* and *S. polaris* sites (Figure 4.1 and 4.2). Rats were most prevalent in *S. polaris* herbfields, with the only evidence of them in *P. hookeri* herbfields occurring at P4 and P5. There appeared to be no seasonal pattern to rabbit, slug and rat activity during the study.

Table 4.5 shows leaf deposition on to seedling plots occurred at four *S. polaris* sites, with half of the seedling plots at S3 experiencing leaf deposition. Only one plot,

within the densest *P. hookeri* population (P3), was obscured by leaf deposition during the study, which occurred in March.

Table 4.5. Proportion of plots within megaherb populations that had 50% or more of the plot covered through leaf deposition in March 2001 (when leaves began to senesce). N.B. only one *P. hookeri* plot (P3) had leaf deposition therefore it is the only P site listed.

Sites	Proportion of plots affected
S1	0.17
S2	0.42
S3	0.55
S4	-
S5	0.08
S6	-
P3	0.08

Microclimate profiles within a *S. polaris* herbfield are shown in Figures 4.4 and 4.5. The cyclic nature of the light environment, representing day (peaks) and night (troughs), is shown in Figure 4.4. Figure 4.5 shows variation between air and soil temperatures in both environments.

Canopy air temperature and gap air temperature appear similar, with canopy air being up to a degree higher on some occasions during the middle of the day. Soil temperature beneath the canopy was the most constant of all parameters measured. The most temperature variation occurred in gap soils, where the highest temperatures were recorded (22.5 ^{0}C) and some of the lowest (1 ^{0}C).

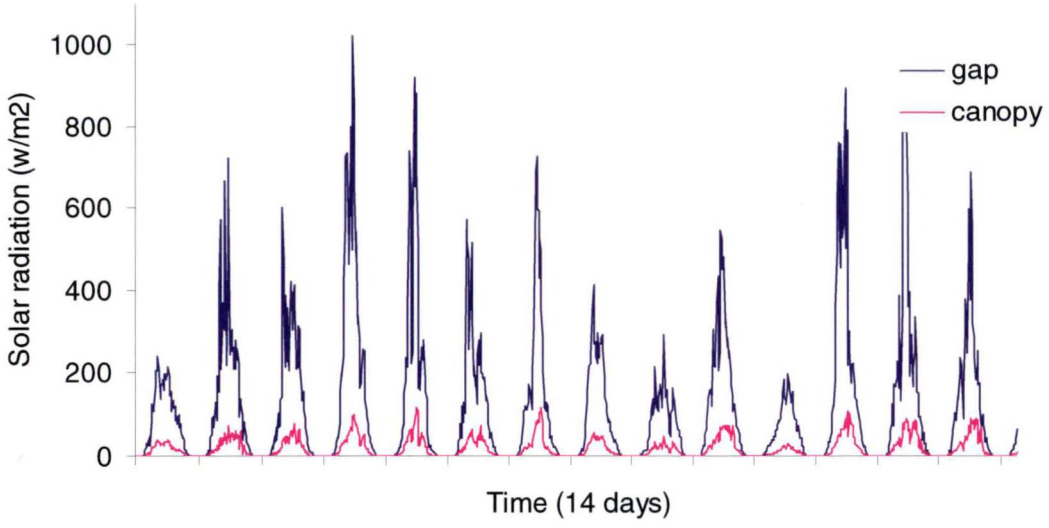


Figure 4.4 Incoming solar radiation in a *S. polaris* herbfield during November. Blue indicates the gap micro- environment whilst pink represents the under canopy micro-environment

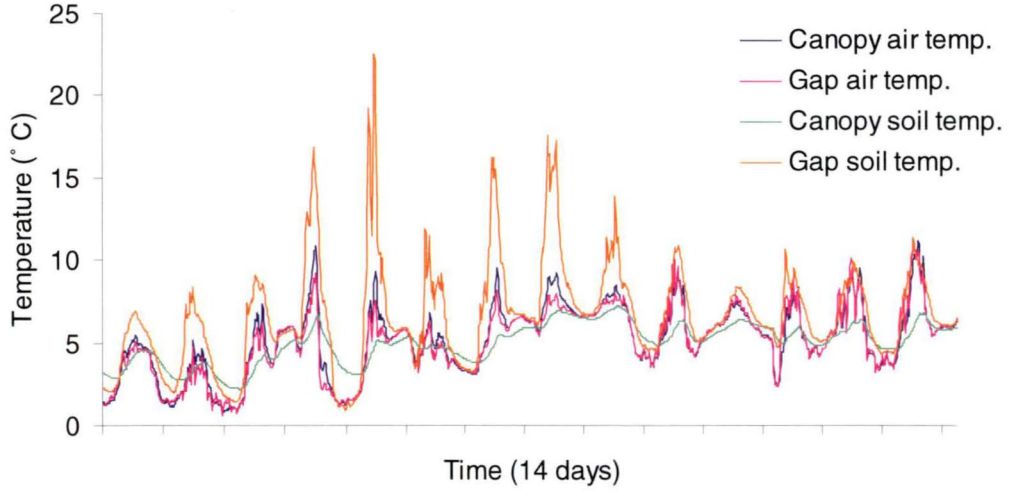


Figure 4.5 Microclimate profile within a *S. polaris* herbfield indicating the differences between air and soil temperature inside and outside of the leaf canopy.

Discussion

Megaherbs on Macquarie I. have very high seedling densities when compared to other plant species (Gartner et al. 1983; Cooper et al. 2004; Llambi et al. 2004; Moles and Westoby 2004). Previous studies have observed seedlings of both species *in situ*, (Jenkin and Ashton 1979; Meurk 1982; Scott 1995; Bergstrom et al. 1997; Copson and Whinam 1998), but this is the first study to quantify *P. hookeri* and *S. polaris* seedling emergence, densities and subsequent survivorship in the field.

Seed deposition

Megaherbs naturally disperse their seed in large piles amongst adult plants due to the top-heavy nature of the inflorescences and racemes. The seed rain study indicated that most megaherb inflorescences do not fall far from parent plants (Chapter 2); however, on some occasions several *S. polaris* seeds dispersed up to a kilometre away from parent plants. The current study also shows that megaherb seeds can disperse away from parent plants as is evident by the presence of seedlings within control plots, despite the fact that there were no seeds visible within the plots. It is also possible that seeds were present in the soil from the previous year (*S. polaris*) or at least 2 years previous (*P. hookeri*). Wind is most likely responsible for seed dispersal of both species as *P. hookeri* has pappused fruits and *S. polaris* inflorescences were observed being wind dispersed. Such seed dispersal explains the occurrence of occasional isolated megaherb individuals outside of herbfield communities, as observed during the study and as described for neighbouring islands (Foggo and Meurk 1981; Meurk 1982).

Seedling emergence

Walton (1979) stated "once a seed finds the right ecological niche in which to germinate it does not necessarily result in each seed producing a mature plant". He suggested that seeds in the subantarctic environment suffer competition effects from the nearest neighbours if they germinate in an established community, or if they fall on bare soil, and that seed fate is governed by soil microtopography and microclimate. This study has shown that where accumulations of seeds occurred there was a high chance of seedlings emerging, although, high concentrations of seeds did not always result in high seedling densities.

Stilbocarpa polaris possesses a thick pericarp protecting the seeds inside and all previous attempts to germinate the species have failed (Bergstrom et al. 1997; Tweedie 2000). Seed coat inhibition influences seed germination in another subantarctic megaherb, *Pringlea antiscorbutica* (Dorne 1977). At the onset of the study it was predicted that only old seed from previous seasons would produce seedlings, as these seeds were more likely to have undergone some form of mechanical or chemical abrasion. However, *S. polaris* germinants emerged from the newly created seed piles which were only three to four months old. It is possible that seedlings could have emerged from an existing older seedbank, below the piles, but this is unlikely. Given the structure of the piles it is likely that only the seeds in the upper surface would germinate and survive due to light conditions and the dense nature of the pile.

Seeds of temperate, arctic and subantarctic species are generally classified as having a physiological dormancy (Dorne 1977; Walton 1977b; Baskin and Baskin 1998)

meaning they have a physiological inhibiting mechanism of the embryo, preventing radicle emergence. The requirements to break such dormancies are varied and complex. The seedbank environment is moist and undergoes freeze-thaw which may break down the pericarp. The role of soil-borne fungi and invertebrates is not known. Further studies are need to investigate germination inhibition.

Macquarie I. has a constant climate with very little seasonal variation. Daylength, or photoperiod, is the major climatic difference between winter and summer, influencing the amount of solar radiation reaching the soil surface and slightly increasing air temperatures in summer months as shown in microclimate profiles (Figure 4.4 and 4.5).

The time lag between dispersal and germination in *P. hookeri* and *S. polaris,* may be due to this subtle climatic variation or may be a developmental requirement of post-dispersal seeds. The earlier onset of germination in *P. hookeri*, may be due to its earlier dispersal, in autumn, than *S. polaris* which does not disperse until early winter (Chapter 2). The time lag between dispersal and germination, for *S. polaris* and *P. hookeri* seeds, is similar to *Pringlea antiscorbutica* another subantarctic megaherb. On the Kerguelen Archipelago *P. antiscorbutica* seeds ripened in February and commence germination in May (Dorne 1977). On South Georgia which is a colder environment seeds of the small herb *Acaena magellanica* took 6 months longer to germinate (from February to December) (Walton 1977b).

Seedling densities

Both species of megaherb had very high seedling densities, and such high seedling densities have not previously been recorded in the subantarctic for any plant species. Several studies in the Arctic have recorded high seedling densities, in one case over 5 900 seedlings m^{-2} (Welling 2002).

Megaherb seedling densities were higher when temperatures were slightly milder, in late spring and early summer, when the mean number of snow days each month and frost days each month are lowest (< 5 days), and photoperiod is increasing (Tweedie 2000) Photoperiod peaks in December (Tweedie 2000), and may trigger germination as has been shown in other species (Baskin and Baskin 1998). Climate data previously collected at S1 (Tweedie and Bergstrom 2000) shows that mean air temperature and soil temperature (below the surface) begin to increase during September and peak during January. Seeds piles formed through rat caching (P4 and P5) had the greatest seedling densities presumably because these piles contained unnaturally high concentrations of seeds.

Of the naturally dispersed seeds, sites with the greatest flowering density had the greatest seedling densities, however, no statistically significant relationship could be found between flowering density (*S. polaris*- inflorescences m^{-2}; *P. hookeri* -raceme m^{-2}) and seedling density. Perhaps quantifying reproductive effort as raceme or inflorescence density is inadequate for determining the reproductive potential of a population. It is likely that a high density of inflorescences (or racemes) reflects optimal growing conditions. The sites with the biggest plants produced the highest seedling densities, presumably as they produced more and possibly bigger fruits. The

site with the lowest *P. hookeri* fruit mass (P7) had the lowest seedling density of all *P. hookeri* sites. Low fruit mass may indicate low seed viability for the population. Given the extreme climatic conditions associated with this high altitude feldmark site it is not surprising that at the upper limit of the species, plants are small and fruit mass and seedling densities are low.

Despite differing aspects, the two low altitude sites S1 and S2 had similar *S. polaris* inflorescence densities. However, the easterly facing, and therefore more protected site (Tweedie 2000) had a lower seedling density. The population contained viral *S. polaris* plants (Skotnicki et al. 2003) and seeds derived from viral parent material were deposited at the site, which raises questions about the virus's impact on seed viability or seedling health.

Seedling mortality

The exact cause of seedling mortality is not known. Environmental attributes such as aspect (Table 4.2a and b), snow accumulation and duration, frost heave, wind chill and solar radiation have all been shown to affect seedling density and survival, (Diemer 2002; Shimono and Kudo 2003) and bigger seeds have been shown to produce seedlings that have higher survival (Kidson and Westoby 2000; Moles and Westoby 2004).

The huge within site variability of seedling survival suggests that some seedling mortality is resultant of micro-scale processes. It is unlikely that the high mortalities observed are resultant of seedling-seedling competition as the sites with the highest *P. hookeri* seedling density, had the lowest proportion of seedling mortality. Seedling

growth was slow, and during the study there did not appear any spatial competition between seedlings in dense plots. Adult megaherb growth was consistent within a site indicating that resources were evenly available across the site. Moles and Westoby (2004), in a review of studies on seedling emergence, identified major causes of seedling mortality in natural seedling populations as drought, herbivory and pathogen attack. The authors summarised that competition from other seedlings accounts for a relatively small proportion of seedling deaths. This study supports their findings as *P. hookeri* populations (P4 and P5) with the highest survivorship also had the highest seedling densities.

There was no evidence of dead seedlings at any site, however, during the study several seedlings were observed with the cotyledons removed. Slugs were recorded at most sites. The slug, *Derocerus reticularis,* is considered a human-introduced species (Frenot et al. 2005). Nothing is known of slug foraging habits on Macquarie I. however, in many other environments *Derocerus reticularis* is known to graze preferentially on seedlings (Hulme 1994; Fenner et al. 1999). If slugs were specialists grazing on *S. polaris* seedlings then slug-induced mortality could be density dependent (ie. seedling density). Davies and Melbourne (1999) found that there was a high probability of slugs (*D. reticularis*) occurring in *S. polaris* herbfields up to 100 m a.s.l. The findings of the current study support this and indicate that slugs are also common in *P. hookeri* herbfields.

Other invertebrates may have impacted on seedling survivorship, as invertebrate density in *S. polaris* communities is high (Davies and Melbourne 1999; Greenslade in press) Greenslade (in press) measured the highest invertebrate abundance in S. polaris

herbfields (80, 000 m^{-2}) with *P. hookeri* herbfields considered to have intermediate invertebrate density (20, 000 m^{-2}). Despite these high invertebrate densities no other invertebrate species were repeatedly observed adjacent to seedlings during the current study, (possibly as slugs are larger than most other invertebrate species). However, Plate 4.5 shows a grazed *S. polaris* seed where the pericarp has been bored through and the seed eaten out. Such damage may be due to a larval stage of an insect exiting the fruit and is unlikely to be due to a rodent (P. Greenslade and S. Chown pers comm.). *S. polaris* seed rain was densest at S3 and many fruits had these visible scars. Examination under a dissecting microscope revealed that the seed had been removed. Leaf litter was deep (20cm) at this site which may influence the insect assemblage and density. Further studies are needed to identify what species predates on these seeds and what the impacts are on *S. polaris* recruitment and potentially other plant species.

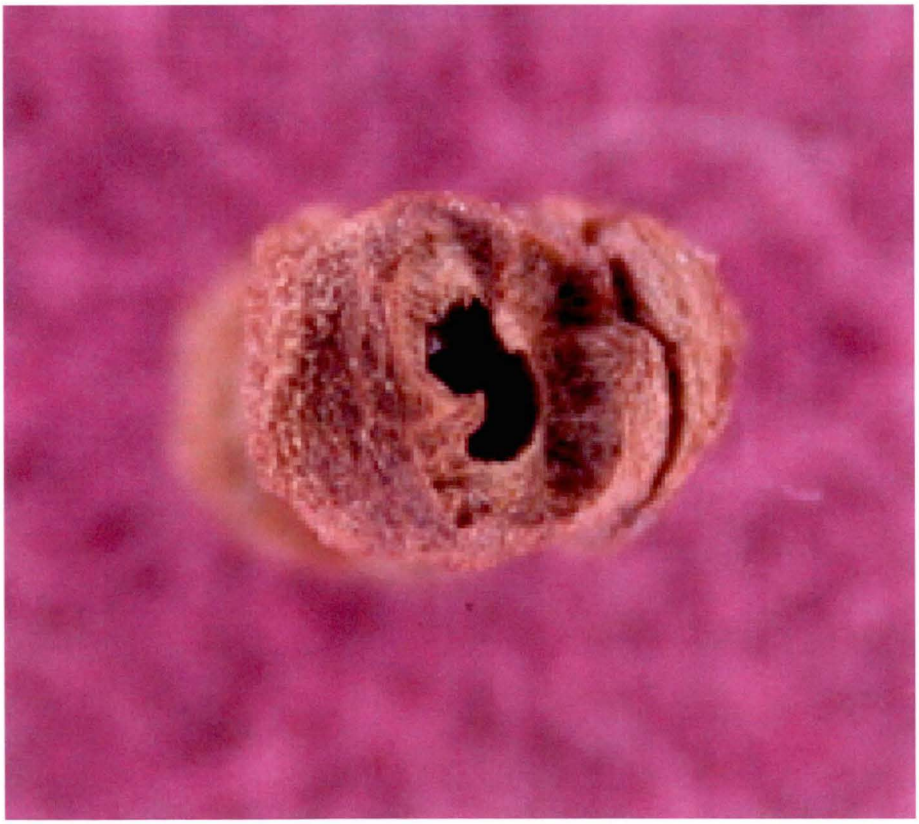


Plate 4.5 A grazed *S. polaris* seed post-dispersal, where the pericarp remains but the seed has been removed.

Previous research has shown that subantarctic megaherbs are not adapted to grazing by terrestrial vertebrates (Ashton and Jenkin 1965; Meurk 1982; Scott 1988; Copson and Whinam 1998; Fenner et al. 1999). Introduced rats and rabbits impacted on *P. hookeri* and *S. polaris* seedling survival through soil perturbation, trampling, and burial. Rats grazed heavily on seeds at a coastal *S. polaris* herbfield (S3) and at two mid altitude *P. hookeri* herbfields (P4 and P5). The quantity and consequences of rats' post-dispersal seed predation on *S. polaris* requires further investigation, Chapter 6 investigates rats' impacts on *P. hookeri.*

Rabbits were widespread across herbfields (Table 4.2), with varied grazing intensity. During the study at P2 and P3, where seedling densities were high, rabbits were observed destroying entire seed plots due to digging and consequent burial. These sites had the highest proportion of plots with complete seedling mortality by autumn 2002. Previous studies (Meurk 1982) showed that following the eradication of feral vertebrates, megaherb seedlings have enabled population regeneration. However, in this study rabbit activity was so extensive, at some sites (S4) the soil surface was displaced thus removing the seedbank. It is unlikely that recruitment will occur rapidly as seeds must now disperse to the site, which is structurally fragile.

Microclimate

Much micro-topographic fluctuation occurs in alpine environments (Shimono and Kudo 2003). The impact of water availability on seedling survivorship is difficult to determine as there was no cost and time effective way to measure soil drying events (drought) at such a small spatial scale across so many sites. There is little seasonal variation in monthly mean precipitation, however, it is lowest in December and

January. Tweedie (2000) found that sunniest conditions occurred when the air is driest and precipitation is lowest (indicating days with low cloud cover). January and February were also found to have the lowest relative humidity (mean and maximum) at S1 (Tweedie 2000). It appears that generally conditions become drier in late summer.

Canopy shading and leaf depositions are natural occurring processes and are resultant of the structure of the standing vegetation. Canopy shading or leaf-filtered light has been shown to reduce germination of some species as the red: far-red light ratio is reduced (Baskin and Baskin 1998). Canopy shading may also reduce soil drying events. Microclimatic data shows that there is great variation between canopy and gap environments. The data show that canopies provide a boundary layer regulating air and soil temperature by reduce wind and blocking incoming solar radiation and thus creating a more comparatively stable microclimate (Figure 4.5). The "gap" soil temperatures were far more variable in the absence of a canopy as there are huge amounts of incoming solar radiation, which heat the soil surface, yet once it becomes cloudy there is no insulation layer to stop heat escaping. Further detailed analysis is required to determine which microenvironment has more energy available to biota.

Despite this variation, no significant difference was found in seedling densities between the canopy micro-environment and gap micro-environment. Thus it appears that soil temperature alone did not influence megaherb seed germination. As leaves expanded during summer months, light availability decreased in many plots. However, no relationship was found between changes in canopy coverage and seedling density. The findings of this study indicate that canopy coverage and

consequently light environment alone do not influence seedling emergence or densities. What is not known is if the light environment influences juvenile plant survival.

Microdisturbance strongly influences seedling survival (Clark and Clark 1989) and seedling plots were monitored for leaf deposition as a litter layer can alter the physical environment of seeds and thus reduce germination (Facelli 1994; Facelli and Ladd 1996; Jensen and Meyer 2001). In a study of fen grassland species Jensen and Gutekunst (2003) found larger seeded species had a lower establishment reduction in the presence of leaf litter than small seeded species. However, at the commencement of this study only seed piles that were visible, ie. not obscured by leaf litter, were selected. Leaf litter is slow to decay on Macquarie I. and therefore it was presumed unlikely that seeds obscured by large megaherbs leaves in early spring would successful emerge.

Both megaherbs species commence leaf shedding in mid autumn. *P. hookeri* sheds the majority of its leaves prior to winter, whilst *S. polaris* sheds mostly big old leaves and retains younger leaves over-winter. Leaf deposition was expected to be greater in herbfields with dense rosettes and abundant biomass, as found in other studies (Jensen and Meyer 2001; Gillman et al. 2004). Although very little leaf deposition was recorded, it was most abundant at the sites with the biggest, densest plants (for both species), and was more prevalent in *S. polaris* indicating that leaf senescence commences earlier than for *P. hookeri.* Only two seedling plots were entirely covered and the seedlings obscured. It is most likely that leaf deposition increased later in autumn and early winter, after monitoring ceased in March 2001, and may have then

contributed to seedling mortality, however, the initially high seedling mortality observed in this study was not due to leaf deposition.

2002

By March 2002, 18 months after the first seedlings emerged seedling survival was low, with over 50% of all plots experiencing total seedling mortality (100% death). However, some seedlings survived, and at some sites there was great within site variability, with seedling mortality varying from 0 to 100% in adjacent plots (< 5m). *P. hookeri* populations that had the highest seedling densities (P4 and P5) in 2001 also had the highest proportion of survivors in autumn 2002. A low altitude *S. polaris* population, which had the highest seedling density in summer 2001, had the greatest seedling mortality in March 2002. Seedling dynamics may differ between the two species, however, it must be noted that this *S. polaris* site had the highest incidence of leaf deposition, rat and slug activity of any megaherb population studied.

Interestingly, a number of new seedling had emerged within *S. polaris* plots between autumn 2001 and autumn 2002. No new seed had been deposited onto the plots and the seedlings had progressed beyond the cotyledon stage, and therefore, the seed was from the previous year (approximately 20 months earlier) and had maintained viability to summer 2002. *P. hookeri* seed piles only produced three new seedlings in a single plot which had since had fresh seed deposited in it (as 2001 had been a masting year). This suggests that *P. hookeri* seed longevity is much shorter. The seed structures are very different and it likely that the thick, hard *S. polaris* pericarp offers more protection than that of the *P. hookeri* achenes.

Jenkin and Ashton (1979) described survival of *P. hookeri* after 12 months as "good in large gaps, poor in small gaps and non-existent amongst closely spaced rosettes", based on their general observations. This study has shown some seedlings do survive amongst closely spaced rosettes, and survival was no lower than that in large gaps. Despite initial high megaherb seedling densities, survivorship was low across all populations. Nonetheless, those few seedlings did manage to survive and were recruited into the population, aiding population survival and expansion.

Vegetative reproduction

Previous research in the arctic and subarctic found that strongly clonal vascular plants have a poorer ability to seedling recruitment than aclonal plants (Eriksson and Erhlen 1992; Welling 2002; Welling et al. 2004). Both species of megaherb are clonal (Jenkin and Ashton 1979; Scott 1995; Copson and Whinam 1998) yet this study has shown that they produce large amounts of seedlings, many of which survive and enter the population as juvenile plants. Interestingly, only one vegetative (clonal) individual's emergence was detected in a megaherb population throughout this study. In one plot (S3) a newly emerged *S. polaris* vegetative shoot had emerged by March 2002. Given the size differences and access to resources of this newly emerged shoot compared to that of seedlings its chances of survival are quite high. Further studies monitoring the survival of such shoots are needed to determine their role in population recruitment.

Conclusion

Previous researchers have observed *S. polaris* and *P. hookeri* seedlings (Jenkin and Ashton 1979; Scott 1995; Copson and Whinam 1998) and shown that recruitment

through seedlings can occur following vertebrate grazing (Meurk 1982; Meurk et al. 1994b). This study has shown that the many seeds dispersed by megaherbs germinate following winter dormancy. Emergence times vary significantly among sites but overall seedling densities peak in the summer. From this it is evident that populations are subject to differing environmental conditions and/or genotypic variation effecting seed dormancy, and emergence. Seedlings are exposed to a range of biotic and abiotic conditions spatially and temporally. Accurate quantification of the environment proved difficult, however, the study has detected that introduced vertebrates have a negative impact on seedling survival. Despite high summer densities seedlings survivorship is low however, given the high initial seedling densities the few seedlings that do survive contribute to megaherb population recruitment.. Similar life history traits are typical in long-lived, slow growing species and have been observed in other species, occupying the same functional group in similar environments (Hennion and Walton 1997a; Diemer 2002). Megaherbs have been selected for in the subantarctic environment as they have massive reproductive outputs. Despite the climate being harsh for seedling survival, producing large numbers of viable seed increases the likelihood that some seedlings will survive and establish, therefore guaranteeing continued megaherb survival.

Chapter 5 Demographic variation in *Pleurophyllum hookeri*

Introduction

Numerous studies have investigated plant life history strategies (Convey 1996a; Convey 1996b; Hodgson et al. 1999; Ehrlen and Lehtila 2002) and perennial herb population structure (Silva et al. 2000; Garcia and Erhlen 2002; Endels et al. 2004; Llambi et al. 2004). However, few have investigated the population dynamics in subantarctic flowering plants (Chapius et al. 1999).

Life history strategies determine a species' ability to maintain a healthy viable population. Each species has strategies that influence a population's dynamics. In order to persist in extreme environments, plants are faced with a choice to "invest in seed production and seed dispersal (sexual reproduction), invest in vegetative propagules (clonal reproduction) or stay where you are as long as you can (the space holder strategy)" (Körner 1999). In order to understand how plants survive in these extreme environments it is crucial to quantify population dynamics and the influence of the environment.

Convey (1996a; 2003) highlighted the importance of understanding species life history traits. Life history flexibility could allow changes in the development and the shortening of life cycle duration in response to climate warming. For example, a change in temperature may result in a change in seed germination, which alters population recruitment and consequently population structure. Little is known of how

life history traits vary amongst populations, and how these interact with local conditions to influence reproduction and population dynamics (Hennion and Walton 1997a). One study which did investigate such traits found that a herb species can have substantial demographic differences between populations over two sites which differ in nutrient and water availability (van Groenedael 1985).

This study aimed to quantify life history strategies of *P. hookeri* at the species' southern limit. Being a long-lived species it has previously been assumed that regeneration is most commonly vegetative (Jenkin 1972); however, this has never been quantified. This is the first study to determine the life history strategies of a subantarctic megaherb. Several populations were investigated across different sites to examine life history flexibility across differing environments, using population matrices. To construct demographic matrix models, estimates of age or size dependent fecundity, survival, growth and shrinkage probabilities of all life stages are required (Forbis and Doak 2004). Given the time frame of the experiment, viability and population growth estimates were not made, they were inferred from existing population structure and performance over 17 months. However, seedling emergence was recorded and therefore this component and the survival and growth of individuals from one summer to the next makes this a dynamic study.

There are numerous methods of constructing life models (Silvertown 1987; Caswell 1989; Silvertown and Lovett Doust 1993) with age or stage structure commonly used. Given the difficulties in determining age of perennial herbs this study has replaced age with size, or stage, as is common with other studies on perennial alpine herbs (Silva et al. 2000; Endels et al. 2004; Forbis and Doak 2004; Zoller and Lenzin 2004).

Caswell (1989) outlined why stage-classified matrices are more suitable than age-classified matrices in herbaceous plants.

Pleurophyllum hookeri is a deciduous, long lived species (Jenkin and Ashton 1979). Flowering only occurs every two or three years as masting events in summer at the peak of vegetative expansion. Seppelt (1984) described the species as "occurring in a perplexing array of habitats and environments". With an altitudinal range spanning from the coast to elevations of 380 m a.s.l., the species exhibits morphological variation in response to altitudinal increases (Taylor 1955; Jenkin and Ashton 1979). At high altitudes herbfields are restricted to sheltered gullies, which are typically north facing, although some small isolated individuals occur in exposed feldmark areas. Other environmental attributes, such as waterlogging can influence species performance (Jenkin, 1975; Rich 1996). Chapter 3 describes the species' habit and resource allocation across habitats. An obvious patterning of rosettes can be seen in some populations. Several researchers have attempted to measure and identify determinates of such patterning. Jenkin and Ashton (1979) attributed it to drainage, exposure, altitude, and a balance between seedlings and vegetative reproduction. Rich (1996) attributed striped patterns within the mire community at Handspike Corner, Macquarie I. to peat bulk densities and subsequent waterlogging.

The study aims of this study where to:

- determine the population structure of *P. hookeri* over different sites
- determine if fecundity varied over different sites
- investigate the role of seedlings in population recruitment
- determine if survivorship is similar across life stages.

Materials and Methods:

Four populations of *P. hookeri* were studied from summer 1999/2000 through to autumn 2001 The four sites varied in their physical attributes; topography, aspect, exposure, slope and soil structure. General water regimes were inferred from soil structure as sandy and mineral soils are free draining, whilst peaty, organic soils hold water. For mire vegetation (P1) the water table is visible on the surface. Areas of accumulated beach sand (P3) or feldmark (P7) where soils consist of minerals and rock particles, are typically dry unless there has been recent rain or snow melt, when they are moist but free-draining. Proximity to animal sources strongly influences soil nutrient availability (Erskine et al. 1998). P2 was the closest site to a penguin colony, however, the remaining three sites all had a penguin colony within approximately one km. Prevailing winds and altitude influence nutrient deposition from these colonies. See Plate 4.1 in Chapter 4 for site locations.

Community & Population Structure

During peak growth in February 2000, *P. hookeri* population attributes were measured across the four populations detailed above. Single 5 m x 5 m plots were established in each population, these were then divided into 25, one metre by one metre quadrats. In each of these quadrats, community composition was determined by recording percentage cover of all species present, these were then averaged across the site to give an overall plot coverage.

The number of *P. hookeri* seedlings, juvenile plants (those that were <5 cm in diameter) and adult plants were recorded in each quadrat and the diameter and height of every adult rosette was measured. The plots were re-measured the following

summer in February 2001. The summer of 1999/2000 was a masting event and the number of racemes and their height was measured per rosette.

Plants were grouped into diameter size classes starting from <5 cm (juveniles) and then in increasing increments of 10 cm. The proportion of each size class of the total number of plants within the plot was calculated for each year. The proportion of flowering plants was measured in the masting year.

Population stage transition matrices

Matrix models were created by comparing the population structure of the fixed plots at each site over two consecutive summers. By comparing the size class distributions of a population between seasons the probability of transition from one stage to another was determined. Silvertown (1987) refers to recruitment as the transition from a juvenile stage to reproductive stage; however, in this study recruitment refers to initial recruitment where an individual enters the population beyond seedling stage.

Past recruitment events were determined based on population structure. Current recruitment into the population was determined by measuring the probability of seedling transition to juvenile from one summer to the next, and of juvenile survival. Mortality within populations was measured by the disappearance of individuals between seasons and asexual recruitment was assessed by the appearance of new adult plants.

Seed production

Fecundity was determined at a site level with inflorescences from five randomly chosen flowering rosettes harvested at each site (summer 2000). The samples were then air-dried at 40°C then the total amount of seed produced per plant weighed. This value was then divided by the number of racemes for the plant giving mean fruit weight per raceme (g/raceme). To determine the total weight of seed produced per site this value was multiplied by the total number of racemes for the site (R), thus giving (g/raceme) x R. A hundred seeds of each sampled plant were weighed to obtain a mean seed weight (S). An estimate of the number of seeds produced at the site was determined by the following equation:

$$N = \frac{[(g / raceme) * R]}{S}$$

Results

The relationship between height and diameter of rosettes was investigated and a strong positive relationship was found (Figure 5.1), consequently only diameter has been used to define size class.

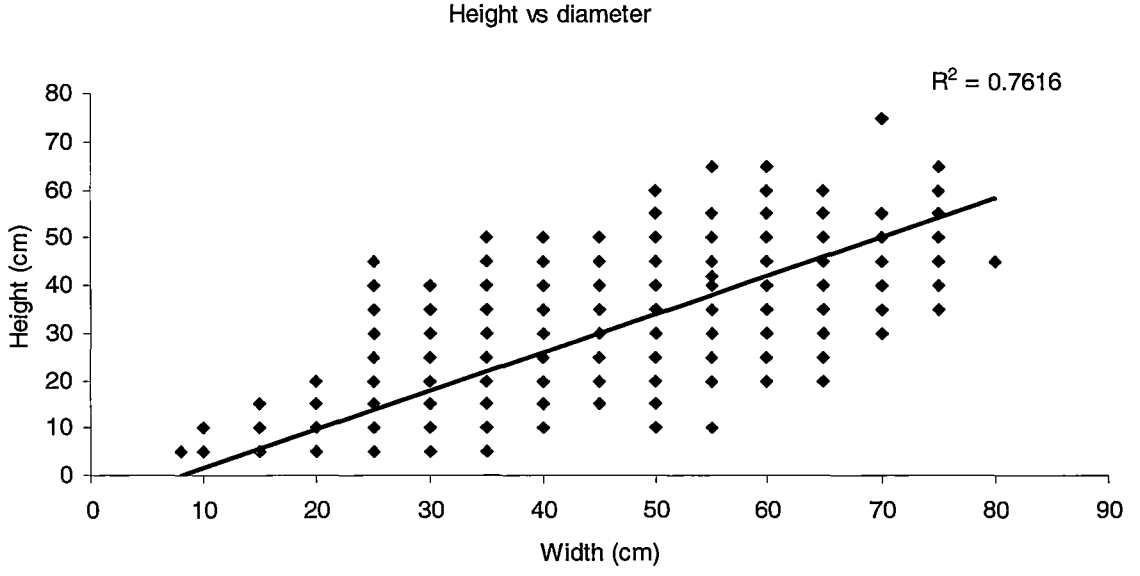


Figure 5.1. The relationship between plant height and plant width in *P. hookeri* across all (four) sites. The R^2 value shows that diameter is a good indication of plant size.

Community Structure

Species richness varied across sites, P1 was the most speciose site (Table 5.1). P2 supported nine vascular species, P3 and P7 were the most depauperate sites each supporting seven vascular species. *P. hookeri* dominated at P1, P2, and P3, while P7 was dominated by *Azorella macquariensis* where it had 80% cover. Vegetation cover was consistently great across all sites, with some variation in vegetation height. However, at all sites *P. hookeri* was the tallest species. Table 5.2 shows P1 and P7 supported low statured vegetation, with *P. hookeri* reaching 20 cm to 15 cm in height (respectively), while at P2 and P3, *P. hookeri* stood at 55 cm and 75 cm high respectively. At P3 all other vascular species were restricted to very small megaherb canopy gaps where they had <10% cover. At the upland plateau herbfield (P7) *A. macquariensis* formed tight continuous cushions covering the majority of the site. Other species grew in small bare gaps or where the cushion had died, however, *P. hookeri* had colonised the majority of available space. Plates 5.1, 5.2a, 5.2b, 5.3, 5.4 show the variation in population structure across the sites.

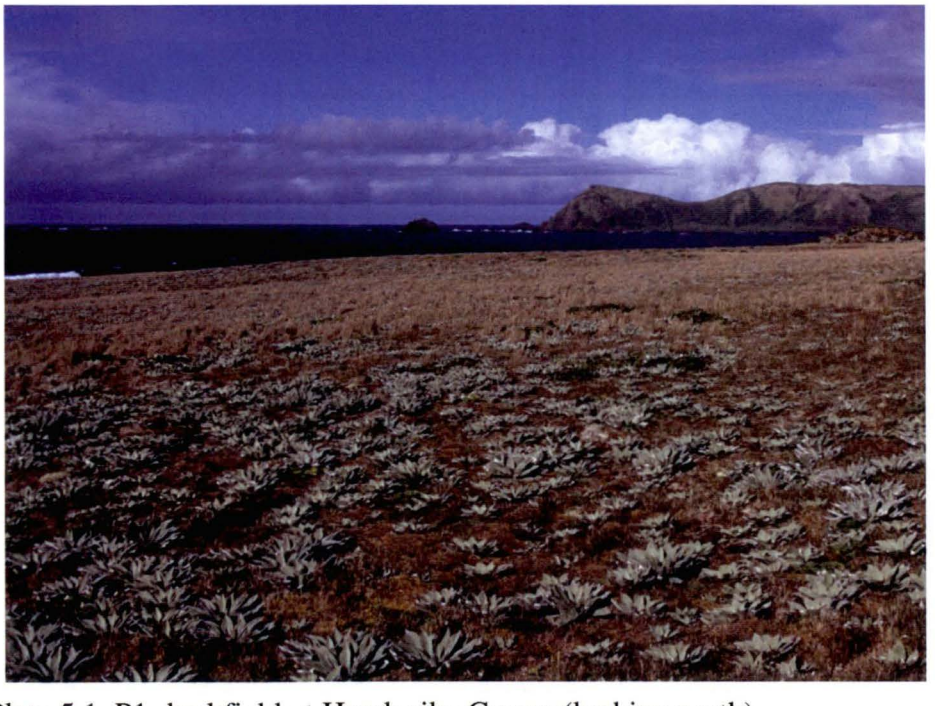


Plate 5.1 P1 -herbfield at Handspike Corner (looking north)

Plate 5.2a P2 -herbfield at Green Gorge basin

Plate 5.2b Green Gorge basin (P2) with herbfield visible as the pale green patch with overland walking track passing through it (looking south west)

Plate 5.3 P3 -herbfield along the 4ways track

Plate 5.4 P7- feldmark/herbfield at Windy Ridge (looking west)

Table 5.1. Community vegetation description of each site

	P1	P2	P3	P7
Attributes	Handspike	Green Gorge	4ways	Windy Ridge
Elevation	15m	15m	190m	370m
Aspect	North to southwest	East	Southwest	North
Exposure	High	Low	Medium- High	High
Slope	Flat	Flat	Steep	Steep
Vascular species richness	13	10	7	7
P.hookeri cover	60-70%	40-50%	100%	20%
Other dominant spp.	*Coprosma perpusilla* (20-30%)	Mixed small spp. (10% each)		*Azorella macquariensis* (80%)
Bryophyte cover	10%	25%	<10%	<10%
Community type	Mire-Herbfield	Herbfield-Mire	Herbfield	Feldmark
Herbfield classification (following Taylor 1955)	*Pleurophyllum-Coprosma*	Ecotone Herbfield-fen	*Pleurophyllum – Cerastium* assoc.	*Pleurophyllum - Azorella*

Table 5.2. Population attributes of *Pleurophyllum hookeri*

Population Attributes	P1 15 m a.s.l	P2 15 m a.s.l	P3 180 m a.s.l	P7 370 m a.s.l
ROSETTES				
Mean density/m^2	15.7 ±2.1	11.6 ±3.4	10.8 ±2.1	4.5 ±2.1
Mean diameter (cm)	28.5 ±5.3	31.5 ±5.6	49.5 ±7	24.4 ±4.8
Maximum diameter (cm)	40	75	75	40
Mean height (cm)	12.3 ± 3.5	19.6 ±4.4	43.4 ±6.6	9.4 ±3
Maximum height (cm)	20	45	75	15
FLOWERS				
% of adult plants flowering	24	27	58	46
Mean no. of flowering plants /m^2	3.8 ±1.9	2.9 ±1.7	6.3 ±1.5	1.9 ±1.4
No. of flowering individuals	93	72	151	48
SEEDS				
Weight of 100 seeds (g)	0.127	0.112	0.153	0.093
Mass of seed produced/ site (g)	257.4	761.4	2591.2	116.45
Number of seeds per site	202 677	679 464	1 693 594	125 161

Population Structure

Plant diameter, height and densities varied across all sites. Rosettes were largest at P2 and P3, being up to 80 cm in diameter (Figure 5.2). The maximum diameter recorded at P1 and P7 was 50 cm. The most abundant size class at P1 was 30 cm; at P7 it was 25 cm. This did not vary between years. Figure 5.2 shows populations at P1, P3, and

P7 had similar distributions, with only a few small plants and many adult plants. At P2 there were plants in all size classes ranging up to <80 cm, with most occurring in the 10 cm size class. There was a bimodal distribution of size classes within this population. Figure 5.3 shows that despite P7 and P1 having similar sized plants, the spatial density of the rosettes (rosettes m^{-2}) varied. High altitude P7 had the lowest density of *P. hookeri* plants while low altitude P1 had the highest density of plants.

Flowering

At P2 and P7 only the bigger plants flowered, while at P1 and P3 all flowering plants exhibited similar flowering effort. The minimum size of flowering plants varied across sites, at P7, P1 and P3 it was 10 cm, 15 cm and 20 cm respectively. Therefore, plants that were 10cm or greater were classified as adults, as flowering indicates adulthood. At P2 only plants that were 30cm in diameter or greater flowered. At a population level the greatest proportion of flowering plants occurred at P3, where 58% of rosettes bore racemes; followed by P7 (43%) with P2 and P1 having 25% and 25% respectively. Plants at P3 also had the greatest mean number of racemes per rosette, (Figure 5.5). Plants at P1 had the lowest mean number of racemes per rosette (1.7); however, the fruit mass per raceme was greater than plants at P7.

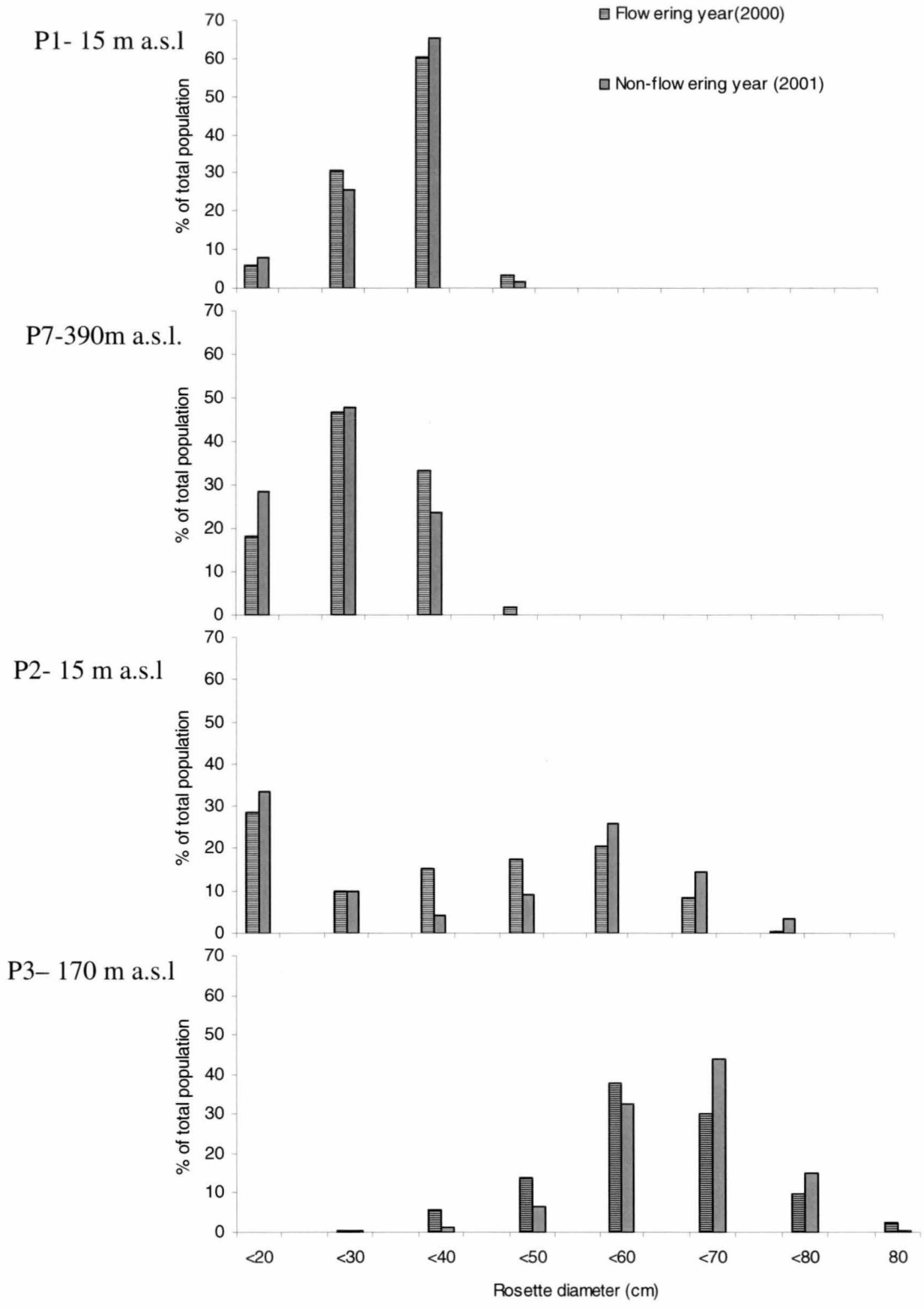


Figure 5.2 Size class distribution of *P. hookeri* rosettes across four sites. The banded columns represent measurements from the flowering year (2000), and the filled columns are those from a non-flowering year (2001).

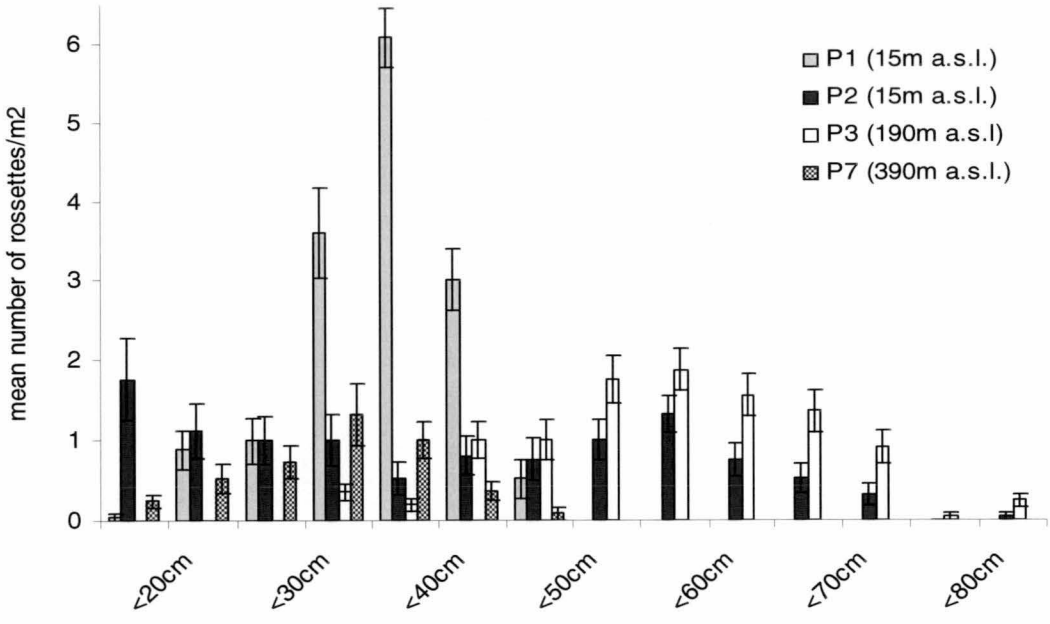


Figure 5.3 Mean spatial densities of different size classes (5cm intervals) per quadrat across sites in 2000.

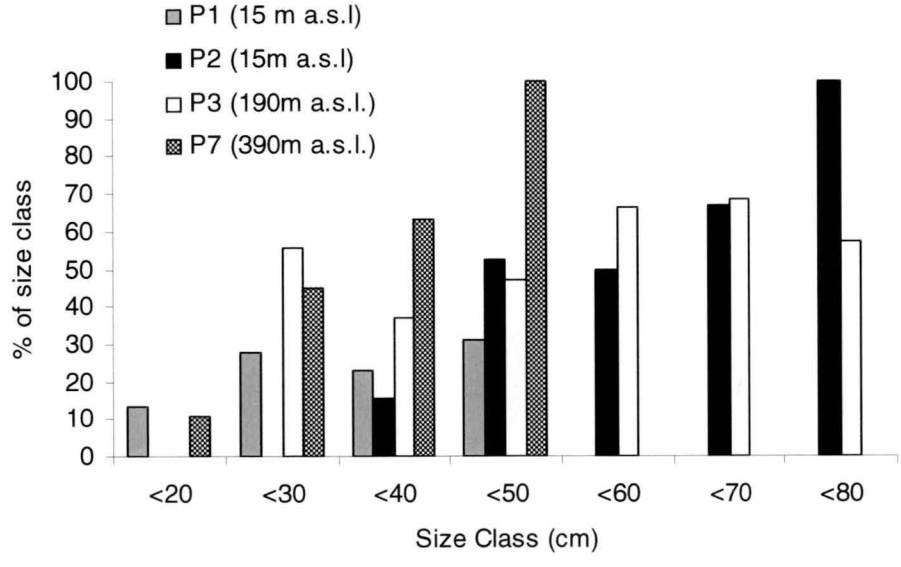


Figure 5.4 The proportion of *P. hookeri* plants flowering within each size class across all sites in 2000.

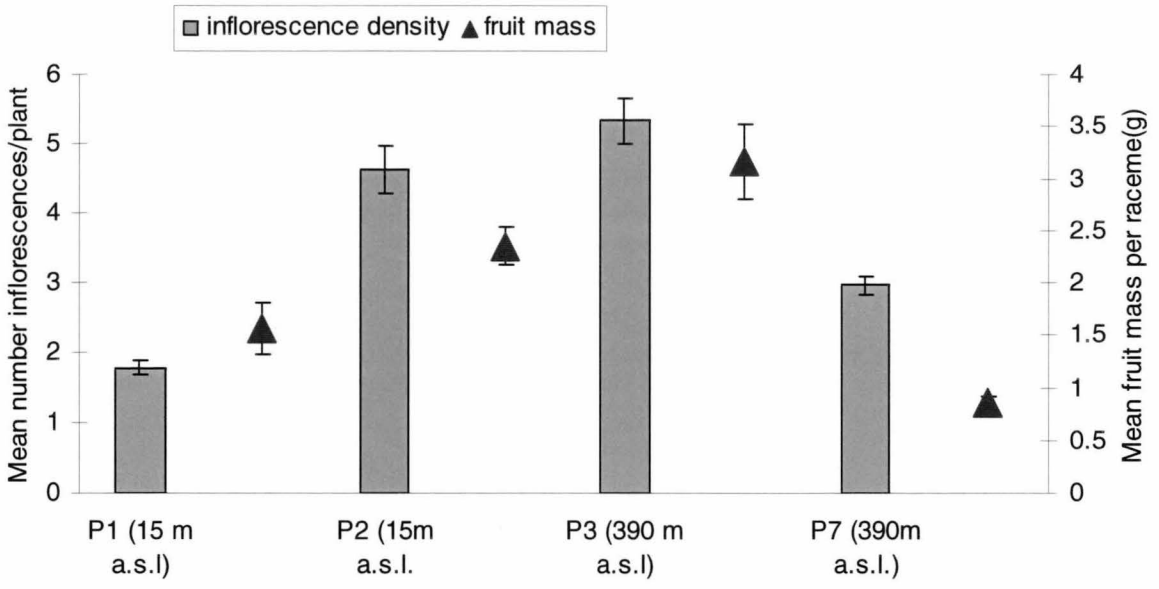


Figure 5.5 Total seed mass of *P. hookeri* across sites, where columns representing the mean number of racemes per plant at the site, and triangles represent the mean fruit weight per site.

Population stage transition matrices

From the matrix tables (Table 5.3 a-d) it is evident that the most recruitment into a population occurred at the low altitude herbfield (P2) where the most seedlings (231) emerged in 2001. P3 had very little seedling recruitment into the population. The absence of juvenile and smaller sized plants in the population shows that recruitment from seed had not occurred for many years. The population at P1 was similarly structured, however, vegetative expansion resulted in 11 new small rosettes while at P3 only one vegetative recruitment event occurred.

Table 5.3 Population stage transition matrices for *P. hookeri* populations at P1, P2, P3. P7, where stage classes range from seed to 80+ cm in diameter. The table shows the probability of each stage class's transition and survival over a year from autumn 2000 (columns) to autumn 2001 (rows) ie. the table reads down. The final row shows the probability of each stage class (autumn 2000) dying within the year. The number of individuals entering the population through vegetative expansion and the amount of seed produced at each site are also shown. Numbers in bold indicate the minimum size (stage class) of flowering for each site.

P1

Seed production = 202, 677

Vegetative recruits = 13

		Seeds	Juvenile	<10	**<20**	<30	<40	<50	<60	<70	<80	80+
Probability	Seedlings	0										
of size	Juvenile		0									
class	<10			.25								
transition	**<20**			.75	.14	.51						
	<30				.85	.49						
	<40						1.00	.71				
	<50							.29				
	<60											
	<70											
	<80											
	80+											
	DEATH	1.00	1.00									

P2

Seed production = 679 464

Vegetative recruits = 0

		Seeds	Juvenile	<10	<20	<30	**<40**	<50	<60	<70	<80	80+
Probability	Seedling	<.001										
of size	Juvenile		.04									
class	<10			.25								
transition	<20			.06	.97							
	<30				.03	1.00						
	<40						.28					
	<50						.64	0				
	<60							1.00	.5			
	<70								.5	.62		
	<80									.38	1.00	
	80+											
	DEATH	0.999	0.96	0.69			0.08					

P3

Seed production = 1, 693, 594

Vegetative recruits = 1

		Seeds	Juvenile	<10	<20	**<30**	<40	<50	<60	<70	<80	80+
Probability	Seedling	<.001										
of size	Juvenile		0									
class	<10			0								
transition	<20				0							
	<30					0						
	<40					1.00	0					
	<50						1.00	.03				
	<60							.97	.53			
	<70								.47	.89		
	<80									.11	.99	.83
	80+										.	.17
	DEATH	0.999	1.00									

P7

Seed production = 121, 161

Vegetative recruits = 0

		Seeds	Juvenile	<10	**<20**	<30	<40	<50	<60	<70	<80	80+
Probability of size class transition	Seedling	<.001										
	Juvenile		.31									
	<10		.07	.43								
	<20			.57	1.00	.16						
	<30					.84	.31					
	<40						.69	.99				
	<50							0				
	<60											
	<70											
	<80											
	80+											
	DEATH	.999	.62									

Juvenile plants, plants which are between the seedling and <10 cm class, have lower survival than adults, with 38% surviving at P7 and none surviving at P1. Survival was high for all adult plants across all sites between growing seasons, with no death observed. Once plants at P7 and P1 grew to >10 cm diameter their survival was high. Plant survival at P2 was high (> 90%) once plants reached the >20 cm size class. Smaller plants had lower survival, with 31% and 4% for <10cm and juvenile plants respectively. The population consists of a range of plants, from seedlings to large flowering adults 75 cm in diameter. This population appears to have had regular recruitment events.

The matrix tables show that once adult plants become large the likelihood of increasing in size the following years is reduced. Once plants started flowering at P2 and P3 they increased in size from year to year until they reached the >60 cm size

class, where most stayed the same size (> 60%). However, at the exposed low altitude population (P1) plants do not increase in size after first flowering. There appears to be a growth lag following flowering and bigger plants within the population (> 40cm) did not increase in size. Interestingly for the largest plants within the population (> 50cm) there was a 70% chance of size reduction following flowering. Adult plants within the high altitude plateau population (P7) did not increase in size between seasons. Plants <30 cm in diameter were more likely (84%) to stay the same size with the remainder reducing in size. For the two largest size classes (> 40cm and > 50cm) all plants reduced in size with some appearing to drop two size classes (100% for the 50 cm).

Discussion

Many studies have investigated plant population growth rates, stability and viability, and identified factors which influence these processes. The majority of these studies were conducted over long periods of time tracing the growth, survival and reproductive output of individuals within populations. There are limits to such studies on a species which flowers once every few years, has low mortality and recruitment rates and is conducted over 17 months. Logistic and shipping constraints make it difficult to revisit subantarctic sites. While this a short term study of *P. hookeri* population dynamics, it does provide data on recruitment events and population structure of *P. hookeri.*

The study shows that *P. hookeri* demographic processes varied between populations. The waterlogged mire/herbfield dominated by *P. hookeri* (P1) was characterised by

small, low plants. The mean rosette diameter at the site was similar to that of a low altitude herbfield (P2) and a high altitude herbfield (P7). Population structure at P1 was similar to that of the population at high altitude P7. However, despite plants being similar in size, their spatial density was greater at P1 than P7 (Figure 5.3). P1 has greater niche availability in the absence of the cushion plant *Azorella macquariensis* which dominates at P7.

The population at P1 had the least seedling recruitment of all sites as seen in Table 5.3a this site had the fewest inflorescences per plant but it did not have the lowest seed yield (mass in grams) (Figure 5.5). Being the most species rich site, the low seedling recruitment may be due to the competitive exclusion from surrounding species. Lichen cover was greater at this site than any other, but it is not known what influence lichens may have on seedlings. *Coprosma perpusilla* with its prostrate habit creating thick, dense mats covers 20-30% of the site. The presence of *C. perpusilla* may limit *P. hookeri* seedling establishment. There may also be other environmental factors which influence seedling establishment, as discussed in Chapter 4.

Thirteen new plants emerged vegetatively through dichotomous division of the rhizome in the non-flowering year at P1. The growth rate of such an emergent plant is not known, but these new plants were <20cm in diameter. Interestingly biomass allocation studies (Chapter 3) found that *P. hookeri* plants growing at the site had the greatest proportional biomass allocation to rhizome tissue of any other site. The site's waterlogged nature and associated low nutrient availability may influence plant growth more than altitude, which influences air temperature.

The population structure and plant size of the low altitude herbfield (P2) were very different from other sites, even the population of similar elevation (P1). There were very large plants within the population, ranging up to 75 cm in diameter, however, the mean diameter for the population was much lower. The site was a moist sheltered herbfield situated in a basin protected by hills on all sides except the east. Such protection may be why plants grew bigger and had a greater fecundity than plants at similarly low altitude P1. All large plants flowered, however, at a population level reproductive output was less than that of the mid-altitude herbfield (P3). It is possible that nutrient availability varied between sites and P2 may have had a lower reproductive output due to nutrient limitation. Further studies are needed to investigate the nutritional requirements of flowering.

Populations stage matrices show that P2 had a unique population structure with a large number of both small and large plants, suggesting changing recruitment events over time. Jenkin (1972) suggested that population recruitment varies along a moisture gradient, with *P. hookeri* recruiting via seedlings in wet areas, and undergoing vegetative expansion in dry sites. The assumption was made that bryophytes, a major component of wet areas (fen-herbfields), offer little competition and a safer seed site, reducing wind disturbance and freeze thaw processes. This may explain the high recruitment observed at P2 and the low recruitment at P1. Both sites are wet but bryophyte cover was higher at P2 and *C. perpusilla* cover was less. The prostrate habit of *C. perpusilla* may restrict seedling establishment. The study has shown two moist sites have different recruitment patterns which is contrary to Jenkin's suggestion.. It is important to note that moisture availability in this study have not been quantified.

Unlike all other sites the most regular recruitment over time appears to have occurred at P2 despite high juvenile mortality. Historical evidence shows that rabbit-grazing pressure has changed over the last 30 years (Copson pers com.) decreasing from the high levels that existed in the mid 60s and early 70s, and increasing again since in the late 1990s. Additionally, highest mortality of seedlings, juveniles and adults occurred in this population, which suggests P2 is the most dynamic (or disturbed) population within the study. No actual dead plants were found, however, as Jenkin (1972) stated, dead plants are rarely found, as most are soon frost-heaved from the soils and blown away.

The population at P3 contained the largest plants with the highest fecundity (both at population and individual level). This implies that conditions at this site were the most optimal for *P. hookeri*, as is discussed in Chapter 3. Table 5.3c shows, despite these favourable conditions very little recruitment into the population had occurred in recent times. The population comprised large mature plants which produced vast amounts of seed yet there was low seedling emergence and high seedling mortality. There are several factors which may influence this high seedling mortality. The viability of the seeds produced at each population is not known, however, given that very few seedlings of any species were found at the site, it is most likely due to edaphic conditions at the site. At P3 a continuous, thick, dense canopy up to 75 cm high blocked light from reaching the soil surface, which would prevent juvenile plants growth. Further, in autumn each year, senescing leaves accumulate on the soil surface. The low species richness and cover (<10%) indicated that conditions at the site are not

conducive for colonisation of any species, even those species that are typically abundant and widespread across the island.

The harshest micro-environment for *P. hookeri* growth was at P7, as indicated by the uniformly small diameter and stature of the plants. Growth was limited by the low temperatures associated with high elevation, wind abrasion due to exposure, nutrient poor soils, freeze-thaw action in mineral soils and the most persistent snow cover of all sites. The site was also subjected to intense rabbit grazing throughout the study.

Figure 5.4 shows that all the biggest plants at the site flowered, however there appears to be a linear reduction in flowering with decreasing size, unlike at some of the sites. Plants at the site produce more inflorescences per plant than plants growing at low altitude site P1; however, the yield of seeds per inflorescence was lower than at P1. Table 5.3d indicates that seedling emergence was low. The presence of seedlings indicates that germination requirements are met at the site. The population had the least number of individuals of all sites. Given the continuous impenetrable cover of *A. macquariensis* it may be that recruitment was limited more by microsite availability than seedling establishment requirements. This is likely given the presence of 31 juvenile plants in the population, indicating that recent recruitment events have occurred. Juvenile survivorship was higher at this site than at P2, which suggests that once a seedling was established amongst the *A. macquariensis* its chance of survival was comparatively quite high. Alpine cushion plants are known to create their own microclimate with higher temperature and water availability than ambient condition (Selkirk et al. 1990b; Zoller and Lenzin 2004). It must be acknowledged that it is not known how old these plants are, and they may stay this size for some time due to the

harsh growing conditions. For example the juvenile cohort at P7 may represent recruitment over a broader time frame at P2, which presumably have a higher growth rate.

Other studies on alpine plants have estimated that individuals of some perennial herb species live to be over 330 years old (Forbis and Doak 2004). The exact age of *P. hookeri* individuals is difficult to determine. Jenkin (1972) estimated an approximate age of small rosettes by counting the number of circumferential ridges along the rhizome. He postulated that a plant from an intermediate altitude (170 m) that was 8-15cm in diameter may be 6-10 years old, and larger plant, 23-41cm in diameter may be 10-40 years old. However, there are limitations to such a model; with large *P. hookeri* plants' ages presumed to be an under estimation, during this study it was observed that the older portions of the rhizome decay. Therefore if anything, Jenkin's age model is an underestimation. Figure 5.2 shows that more than 90% of all plants growing at P3 (170 m a.s.l) were greater than 40 cm in diameter. If Jenkin's age model was applied here it suggests that 90% of the plants at the site are over 40 years old, which is greater than the 19 year predicted life span of (sub)artic and alpine plants (Ehrlen and Lehtila 2002).

In this study, no attempt was made to age plants as no reliable method was discovered. Therefore, variation among sites in environmental conditions is likely to confound comparisons of size classes between populations. However, within a site the assumption was made that small plants are younger.

Jenkin and Ashton (1979) determined that *P. hookeri* mean plant diameter and height decrease, and plant density increases, with increasing altitude. They also stated that increased waterlogging of the substrate generally results in a decrease in rosette diameter. The current study found that the mean rosette diameter at low altitude P1, a waterlogged mire community was less than that of mid –altitude plants at P3. The current study shows that there is much variation in plant density across the island. Mean plant density (per m^2) was not found to increase with altitude, and indeed the lowest plant density occurred at high altitude P7.

Pleurophyllum hookeri is a masting species, which is a population phenomenon that results from the cumulative behaviour of individual plants (Koneig et al. 2003). Long-lived species are less dependent than short-lived species on reproductive systems that ensure reproduction every year (Ehrlen and Lehtila 2002). Mass flowering occurs across the whole island. In 1996, 1999, and 2001 all *P. hookeri* herbfields were observed to support huge amounts of flowers, in 1997 flowers were almost non-existent with only a small number seen on the island despite considerable search effort. The study shows that within masting years flowering effort varied across populations.

Reproductive effort appears to correspond with plant size, as other studies have found in perennial herbs (Garcia and Erhlen 2002) specifically megaherbs (Silva et al. 2000) The biggest plants exhibited the greatest reproductive effort and the minimum size for first-flowering to occur varied across sites and same size classes did not exhibit the same flowering effort across sites (Figure 5.4). The high proportion of flowering plants in the biggest size classes at P7 and P2 is most likely due to their low

occurrence (Figure 5.2). As shown in Table 5.2, both low altitude sites P1 and P2 had low flowering for all adult plants. However, if only plants of minimum flowering size for the site are considered at P2, 44% of these plants flowered.

Plant diameter is a function of leaf length and it is not known what controls leaf length in *P. hookeri.* Plant diameter may have been influenced by initial leaf size, determined by the current season's growth (photosynthesis) or possibly the last season's reserves Flowering exerts nutritional strain on the plants (Körner 1999) so it could be predicted that rosettes would be bigger in non-masting years. The distribution across size classes between years is different, and it appears that in a non-flowering year plants jump a size class as they grow and increase in diameter. This was the case for all sites except P7, where rabbit grazing pressure was extremely high during winter and spring of 2000, and still present in summer 2001. It must be acknowledged that the study has measured progression between summer 2000 and summer 2001, however, whether this is due to flowering vs non-flowering years or merely a passage in time reflecting other environmental factors is not known.

Chapius et al. (1999) found that diameter was not always predictive of first-flowering in *Pringlea antiscorbutica*, a subantarctic megaherb confined to the Southern Indian Oceanic Is. Flowering of *P. antiscorbutica* commenced when most plants reached three or four years of age. The smallest flowering *P. hookeri* plants occur at P7, plants of a similar size did not flower elsewhere. Like *P. antiscorbutica*, diameter of *P. hookeri* is not predictive of first-flowering. It is most likely that productive sites produce large plants in a shorter space of time and therefore age not size determines

first-flowering, consequently the minimum size at which flowering occurs varies from site to site.

The findings of this study suggest that recruitment processes are complex with several environmental variables and perhaps, historical events involved. However, general trends apply at the species level. Like other megaherb species juvenile plants exhibit the most sensitivity (Silva et al. 2000). Once *P. hookeri* plants reach a considerable size (10cm+) survivorship increases markedly. The matrix tables show that the largest adult plants had a 100% survivorship over the course of study.

Silva et al. (2000) found that high altitude Andean rosettes (*Espletia timotensis* and *E. spicata*) produced vast amounts of seed contributing to a large soil seed bank, however recruitment rates were low as was the case in *P. hookeri*. As proposed by Silva et al. (2000), expenditure may be detrimental to population growth however seed banks must be invested in to withstand unpredictable events. While nothing is known about megaherb seed longevity, there may be some input via the seedbank to mass recruitment events, although it appeared that most germination was due to surface seeds (ie. fresh seed). Other studies (McGraw and Vavrek 1989; Misiak unpub.) have found similar seed bank investment in Artic, alpine and subantarctic environments.

The transition matrix tables show that seedling and juvenile plant survival was low, as is common in many plant populations (Silvertown and Lovett Doust 1993; Ehrlen and Lehtila 2002; Forbis and Doak 2004). Recruitment into all populations was also extremely low with most populations predominantly consisting of adult plants. Other

perennial alpine plants appear to have similar demographic patterns. Diemer (2002) investigated life history stages of a perennial alpine herb and found that populations were remarkably stable in the long term.

A major finding of this study is variation in population demography of single species across a range of environmental variables. This is despite these populations occurring on a small island which has an extremely equitable climate. To date most other studies have focused on a population structure at one site (Forbis and Doak 2004). This study is of great significance as it highlights the species' life history flexibility enabling it to occur over a range of environments. *P. hookeri* has very wide ecological amplitude on Macquarie I., wider than most other species that occur there, particularly other large species. The population at P1 exhibited vegetative expansion during the study, which differed from the species' performance at other sites. Further studies are needed to quantify the role of clonal expansion in population growth and sustainment, and to identify the duration of time these rosettes remain attached to an adult rosette. This study has shown that *P. hookeri* is a robust species with the ability to perform differently under environment variation. Recruitment patterns at P2 are most likely reflective of past rabbit grazing pressures.

Grime (1974;) defined a life history model where an established adult phase is influenced by external environmental influences (stress and disturbance) and competition. Grime established that the intensity of these influences determine characteristic ecological behaviour plant performance all of which affect a plant's life history traits. This study has identified some of the life history traits of *P. hookeri* a

large, perennial, locally widespread herb which is restricted globally to the subantarctic environment.

There were many flowering plants at each site and therefore vast amounts of seed were produced. However, despite this large reproductive effort comparatively few seedlings are recruited into the population. The study found that populations are dominated by large old plants which have high survivorship and populations therefore, appear reasonably stable. However, there is evidence of both size frequency histograms and population matrices that recruitment from seedlings does occur particularly in the P2 population. The requirement for new individuals to enter the population is low, however, seedlings are still a vital stage in the species' life history as they provide the opportunity for new individuals to enter the population, maintain genetic diversity, expand the population and increase species survival in the likelihood of stochastic events.

Chapter 6 - The impact of introduced ship rats (*Rattus rattus*) on seedling recruitment and distribution of a subantarctic megaherb (*Pleurophyllum hookeri*).

Austral Ecology (2005) **30**, 118–125

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Introduction

Introduced animals

The complex inter-relationship between native and introduced species on Macquarie Island and other subantarctic islands has been repeatedly emphasised (Brothers and Skira 1984; Crafford 1990; Hunter 1990; Chown and Smith 1993; Scott 1996; Pye 2000; Chown et al. 2001; Copson and Whinam 2001; Pontier et al. 2002). In many situations across the subantarctic, including Macquarie Island, indigenous species have successfully recovered following eradication of introduced vertebrates (Meurk 1982; Meurk et al. 1994b; Micol and Jouventin 1995; Anon. 2001; Copson and Whinam 2001).

There is no history of pastoral activities on Macquarie I., however a number of alien vertebrate pests including rats (*Rattus rattus*), mice (*Mus musculus*), cats (*Felis catus*), European rabbits (*Orycolagus cuniculus*) and Wekas (*Gallirallus australis*), were introduced to the island between 100 and 190 years ago (Copson & Whinam 2001).

Rabbits have caused substantial damage to vegetation on Macquarie Island since their introduction in the 1870s (Jenkin et al. 1982). *Pleurophyllum hookeri* is one of the species that is preferentially grazed by rabbits (Scott 1988; Copson and Whinam 2001). There are currently no native granivorous birds on Macquarie Island however the Red Poll (*Carduleis flammea*), a small, exotic bird species has been observed removing seeds from inflorescences of *P. hookeri.* Its impact on *P. hookeri* dispersal is probably low because the bird population is small (Copson pers. comm. 2003). The extinct ground parakeet (*Cyanoramphus novaezelandiae erythrotis*) may have eaten *P. hookeri* seeds. Subspecies of *C. novaezelandiae*, which occur on the neighbouring Auckland Islands and Antipodes Islands, are typically generalist feeders (Taylor 1985).

Rats on Macquarie Island

Macquarie Island is the southern-most recorded distribution of the ship rat, *Rattus rattus*. Rats were first recorded in the early 1900s (Cumpston 1968), with colonisation resulting from sealing and whaling activities and possibly shipwrecks in the late 1800s. They have previously been recorded from close to the shoreline up to an altitude of 250 m a.s.l. and up to 1 km inland (Copson 1986; Pye et al. 1999). In 2000

we observed rats from below the high tide line to 280 m a.s.l. Their major habitat is coastal tall tussock grasslands where they feed predominantly on shoots of *Poa foliosa* (Copson 1986; Pye et. al. 1999; Copson & Whinam 2001). Additionally, there is indirect evidence that rats eat burrow-nesting petrel eggs and chicks on the island (Carrick 1957; Brothers 1984). The deleterious impacts of introduced rats on plants, invertebrates and burrowing nesting petrels on the subantarctic islands have previously been studied (Pye and Bonner 1980; Brothers 1984; Copson 1986; Micol and Jouventin 1995). Rodents commonly store seeds in shallow surface caches for future consumption (Copson 1986; Pyare & Longland 2000; Longland et al. 2001; Avenant & Smith 2004). During the summer of 1999/2000, we observed rats climbing racemes of *P. hookeri* and carrying away inflorescences and we subsequently discovered what appeared to be caches of *P. hookeri* fruits amongst rosettes in *P. hookeri* herbfields. We monitored caches within two herbfields to investigate the impact of *R. rattus* on *P. hookeri*. We asked a) Once constructed do rats revisit the caches? b) How much seed is removed from plants? c) Ultimately does any of this affect recruitment of *P. hookeri*?

Materials and Methods

Study Site description

This study was undertaken at two sites from March 2000 to March 2002. Rat damage to *P. hookeri* inflorescences was apparent in many herbfield communities around the island, at the start of the study. The first site, Lambing Gully (P 4), (54°29'46.3S, 158°56'34.33E) was a *P. hookeri- Stilbocarpa polaris* herbfield (Plate 6.1A.), situated on an east facing valley at 90 m elevation.

Plate 6.1A. Site at Lambing Gully (P4)

Plate 6.1B. Site at Gadget Gully (P5)

The second site, Gadget Gully (P5), (54°30'31.8S, 158°55'40.2E), was an east facing *P. hookeri* dominated herbfield (Plate 6.1B.), at 210 m elevation adjacent to a creek. At each site a 20 m x 20m study area was defined. Ground searches revealed active rat burrows, characterised by adjacent fresh tracks, surface scratching, scats and chewed segments of *P. foliosa* at both sites.

Rat damage to inflorescences (Lambing Gully)

The degree of damage to *P. hookeri* was estimated at Lambing Gully in early March 2000. The survey was conducted to determine the number of inflorescences and flower racemes that had been removed or destroyed. Eighteen 1 x 1 m quadrats were randomly placed within the *P. hookeri*-dominated site. The number of flowering and non-flowering rosettes, the total number of flower racemes on each rosette, the number of damaged racemes on each rosette, the total number of inflorescences per raceme and the total number of intact undamaged inflorescences remaining per rosette were recorded in each quadrat.

We believe rats were responsible for the removal of seeds as they were observed standing on their hind legs and chewing through the pedicel. Racemes that are damaged by heavy snowfall or ice simply fall to the ground, making them easily distinguishable from the broken rat-chewed racemes. Damaged racemes showed visible chew marks and shredded epidermal tissue (Plate 6.2A). Where the raceme had been removed, the lower section of the inflorescence stem remained attached to the rosette, which enabled flowering rosette density to be measured accurately (Plate 6.2A &B). It is possible that rabbits can damage racemes, however, no rabbit scats or signs of grazing were observed when the damage was first detected during the study.

Plate 6.2 A & B *P. hookeri* pedicels showing evidence of rat damage

Piles of fruits, defined as caches, were larger than aggregations of naturally dispersed fruits, with the piles being from 15 x 15 cm to 30 x 30 cm in size and over 2 cm deep (Plate 6.3). The contents of six randomly selected caches were sampled from Lambing Gully to determine the amount of fruit in a cache. A 20 cm × 20 cm quadrat was placed in the middle of each cache. The material within the quadrat was then removed until the soil surface was exposed. The fruits were air dried at 30°C for 4 weeks, and then weighed.

Cache Study (Lambing Gully and Gadget Gully)

Only caches containing fragments of pedicels and stems with visible rat chew marks (Plate 6.2A & B.) were used as these had obviously been removed from rosettes. Only caches with more than 90% cover of fruit and a fruit depth of 2 cm or greater over the 20 cm x 20 cm area were included in this study.

In June 2000, study plots were defined for 12 randomly selected caches at each of the two sites. Six caches were surrounded by 20 x 20 x 20 cm exclosures constructed of stainless steel frames and 1x 1cm steel mesh in June (Figure 6.4.). The six control caches at each site were marked out with 20 x 20 cm quadrats.

Plate 6.3 Rat created seed cache

Plate 6.4 Mesh exclosure over seed pile

Winter senescence of the mature *P. hookeri* plants, with the dead leaves forming mounds around the plant, had begun at the commencement of the study in March 2000. By mid-winter (late June) these mounds were relatively large, being up to 50 cm deep, and covered the original rosette area. Thus, during winter, caches between the rosettes were easily accessible.

The sites were visited every three to five weeks between June and November, and following that every five to seven weeks, until March 2001, depending upon snow cover. The number of *P. hookeri* seedlings per cache were recorded each visit. All plots were surveyed again during March 2002 to determine seedling survivorship after 12 months.

In conjunction with seedling counts, evidence of rat visitation was recorded, to determine if rats visited the caches. Ground searches within the cache and the surrounding 1 m^2 were conducted. The presence of any fresh rat scats within this area was recorded. Signs of surface disturbance from rat scratching and diggings, and any other animal activity were also recorded.

Data on seedling density were analysed with a repeated measures analysis of variance using general linear model procedures in the SAS statistical package, v.8 (SAS Institute Inc. 1988) Significant effects were analysed with a Ryan-Einot-Gabriel-Welsch *post hoc* comparison (Day and Quinn 1989).

Results

Rat damage to inflorescences at Lambing Gully

Population density of *P. hookeri* was 11.5 rosettes m^{-2} (Table 6.1) at Lambing Gully and in the 1999/2000 summer, 64% of these rosettes were flowering. On average there were five racemes per rosette, and 16.5 inflorescences per raceme (Table 6.1). The highest count of racemes per rosette was 15 and the largest number of inflorescences per raceme was 22. However, 90% of rosettes had inflorescences removed, such that of the expected 577 inflorescences m^{-2} only 27 m^{-2} remained. Therefore, we estimate that approximately 95% of inflorescences were absent from the site.

Table 6.1. Flowering attributes of *Pleurophyllum hookeri* at Lambing Gully (18 x $1m^2$ plots) on Macquarie Island. Values are means with ±se

Attribute	Mean
Number of rosette/m^2	11.5 ±0.1
Number of flowering rosette / m^2	7.1 ±0.5
Number of flower racemes /rosette	5.0 ±0.3
Number of inflorescences / raceme	16.5 ±0.2
Total number of inflorescences remaining/m^2	27.0 ±2.0
% Racemes damaged	89.9 ±1.5

Caches contained an average of approximately 30.3 (±3.4) g of fruit in each 20 × 20 cm cache sampling area, with the maximum cache weight being 44 g. One hundred seeds weighed 0.15 (±0.008) g, therefore the cache plots studied contain 20 000 to 30 000 fruits. Such dense aggregations of fruits were observed only where there was evidence of raceme damage within the herbfields. Furthermore, other populations of *P. hookeri* from which rats were absent did not contain these aggregations of fruits.

Seedling emergence

The presence of exclosures had a significant impact on seedling density (Table 6.2; Figure 6.2). There were no significant differences in seedling density between the sites and no significant site × exclosure interaction (Table 6.2). In addition, there was a significant time effect ($P<0.0001$) and a highly significant time × exclosure interaction ($P<0.0001$), indicating that seedling emergence patterns from June 2000 to March 2001 were strongly dependent upon the presence of the exclosure (Figure 6.2). Maximum seedling density recorded in a plot was 10 500 seedlings m^{-2} in an exclosure and in a control 3 475 seedlings m^{-2}. By March 2002 the mean numbers of surviving seedlings did not differ between the exclosure and control plots (t= 0.87; $P=0.2$).

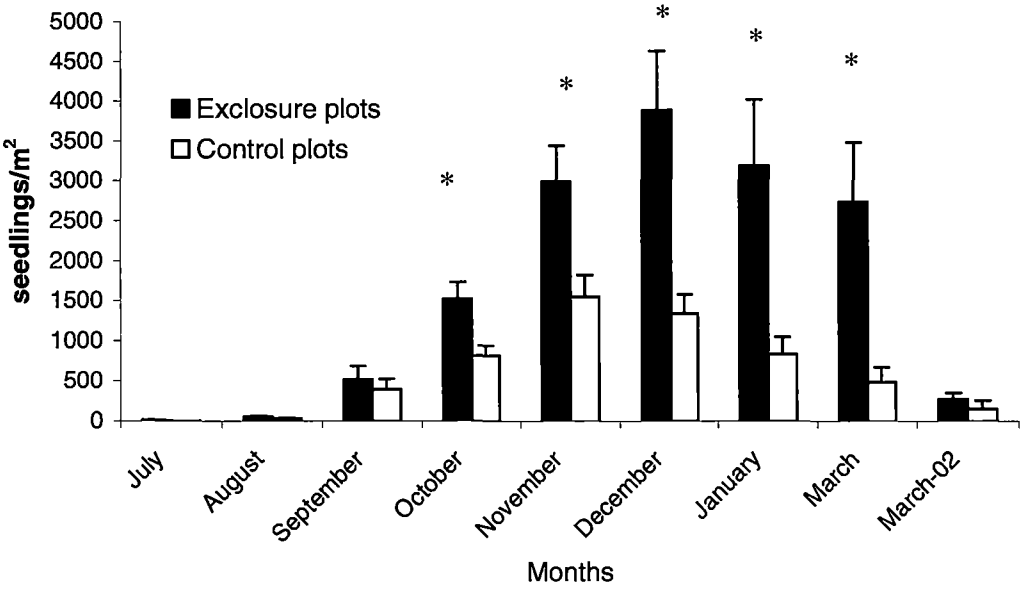

Figure 6.2. *P. hookeri* seedling emergence in exclosure plots and control plots over time, from both sites.

Table 6.2. Results of a repeated measure ANOVA on seedling density of *P. hookeri* at two sites on Macquarie Island. ns = non-significant at P>0.05.

Treatment	d.f.	F	P>F
Exclosure	1,20	8.38	0.009
Site	1,20	0.04	ns
Exclosure × Site	1,20	0.13	ns
Time	8,160	26.7	<0.0001
Time × Exclosure	8,160	7.68	<0.0001
Time × Site	8,160	1.76	ns
Time × Exclosure × Site	8,160	0.20	ns

Seasonal changes in cache usage by rats

The presence of rat scats provided evidence that rats visited caches more frequently in winter months than during the summer (Table 6.3). The degree of activity varied between sites, with Gadget Gully consistently having more evidence of rat activity than Lambing Gully during the winter months. Twelve out of the total 24 caches were visited in July and September 2000. In August nine caches had evidence of rat visitation, and in October there were eleven caches. There was snow present at the sites at the time of sampling for these months. Only one cache had evidence of rat visitation at Gadget Gully during December, and there was no evidence of rats at the Lambing Gully caches. There were no scats found adjacent to caches in January, February and March 2001 (Table 6.3).

Table 6.3. Monthly rat activity in $1m^2$ surrounding caches at two sites on Macquarie Island between July 2000 and March 2001.

	Gadget Gully			Lambing Gully		
	No. of caches with adjacent scats	No. of caches with adjacent scratchings	Total no. of caches with evidence of rat activity	No. of caches with adjacent scats	No. of caches with adjacent scratchings	Total no. of caches with evidence of rat activity
July	10	8	12	1	1	2
August	7	3	9	2	0	2
September	6	5	8	1	0	1
October	10	5	11	1	2	3
November	6	0	6	1	4	4
December	0	0	0	0	2	2
January	1	1	2	0	1	1
March	0	0	0	0	0	0

Discussion

The identification of factors that determine recruitment rates in different plant species is fundamental for understanding plant population dynamics (Eriksson and Erhlen 1992). Changes in recruitment are likely to impact on population size and persistence. Our data show that ship rats visit seed caches and reduce initial seedling establishment of *P. hookeri.* However because of the seedling mortality, rats had no significant impact on recruitment of juvenile *P. hookeri* in our experimental plots.

It is highly likely that rats altered *P. hookeri* dispersal at both sites. Dispersal determines the potential area of plant recruitment and species distribution. Dispersal also affects the rate of gene flow and thus influences genetic structure within and among populations (Nathan and Muller-Landau 2000). Rats affected the dispersal of *P. hookeri* by removing large amounts of fruit from racemes and constructing large piles of seed.

Rats had a major impact on the standing seedbank of *P. hookeri* removing approximately 95% of inflorescences at Lambing Gully. On Marion Island, Chown and Smith (1993) found that mice removed 75% of seed heads from flower stalks of the sedge *Uncinia compacta* by mid autumn. The predicted maximum density of 577 inflorescences m^{-2} at Lambing Gully may be an underestimation, as rats may preferentially select racemes based on larger or smaller size or fecundity, whereas our estimates were based on remaining undamaged racemes. Although we believe rabbits had little impact on *P. hookeri* seeds, it is possible that rabbits also damaged or removed some racemes.

Seasonal changes in cache usage by rats

Seed caching by rodents has previously been observed in the subantarctic (Jenkin et al. 1982; Copson 1986; Chown & Smith 1993; Le Roux et al. 2002; Avenant and Smith 2004). Given that we observed rats removing seeds from *P. hookeri*, we assumed that rats were responsible for the construction of caches within herbfields. Where we found caches constructed there was always evidence of rats, in the form of scats and sometimes burrows. Rat caches of fruits were much bigger than natural fruit piles of *P. hookeri* and the large aggregations of fruit we called caches were absent from populations of *P. hookeri* where there was no evidence of rat activity. Other studies on rodent seed predation used stem or culm scars to measure damage (Kjellsson 1985; Chown and Smith 1993). Kjellsson (1985) described a rodent-induced oblique cut on the fruiting culm and we found similar scars on stems of *P. hookeri* racemes. Rat scats were also often observed on and adjacent to these piles of fruits. However we were unsure if rats would re-visit the caches. Pyare and Longland (2000) state that caches allow rodents to survive extended periods when fresh food

supplies are low or in years when seed production is low. Our results confirm that rats returned to the caches throughout the winter. Attendance at caches declined during spring, coinciding with the emergence and expansion of new *P. foliosa* shoots (Ashton and Jenkin 1965; Jenkin and Ashton 1970), which are the preferred food of rats on Macquarie Island (Copson 1986; Pye et al. 1999). Since initial seedling numbers were greater when rats were excluded from caches we conclude that rats forage on seeds and/or seedlings of *P. hookeri.*

In March 2002 (autumn) rats were again caching fruits, as it was a masting year at the Lambing Gully site. We observed that fresh fruits had been deposited on top of previously constructed caches that had been selected as control plots in 1999. These fresh fruits would have buried any established, two year old seedlings. Thus adding fresh fruit to existing caches may have also impacted on *P. hookeri* recruitment.

Impact of rats on P. hookeri recruitment

Overall seedling density was greater when rats were excluded from caches and this difference was particularly pronounced during the early summer. Greatest germination occurred during early spring, when temperature, daily hours of sunshine and daily net solar radiation are all increasing (Tweedie 2000).

In autumn (March) 2001 the significant difference in seedling density between control and exclosure plots indicated that, regardless of any other environmental parameters, rats caused a decrease of seedling survivorship between mid summer and autumn (Figure 6.2). Thus, the exclusion of rats from the caches they constructed in autumn 2000 allowed for greater initial establishment of *P. hookeri* seedlings. However in

March 2002, 18 months after initial emergence, there was no significant difference between controls and exclosures in seedling density. Several factors may have contributed to this; for example, environmental conditions may not have been optimal for substantial seedling survivorship. In addition, conditions of a rat cache are not ideal conditions for plants due to the impact of competition from such high densities of germinating fruit. Further studies are required to determine the long-term survival of seedlings in cache environments, as they are not the result of typical dispersal conditions.

Pleurophyllum hookeri herbfields have not been identified as rat habitat on Macquarie Island prior to this study. The predominant rat habitat is tall tussock grasslands, where they breed by creating burrows in the peaty tussock pedestals (Pye 2000). The mean home range of breeding rats in tall tussock grassland is 0.114 ha (Pye 2000). Their presence in herbfields, observed in this study during winter and autumn, may reflect a seasonal change in distribution as at these times they are not confined to nest sites. A habitat and distribution study in 1978 (Copson 1986) found no rats in herbfields. However, rabbit grazing was severe in herbfields at this time and consequently there was very little vegetation cover (Copson & Whinam 2001), which may have made it unsuitable rat habitat. Rats may also move into herbfields following an increase in density.

We have shown the impact of an introduced vertebrate on a plant species that has high conservation value. Rats altered dispersal and short-term population recruitment. Our study highlights the need for long-term monitoring as short term significant effects of rat access were not sustained over a longer period. Also rat impact on recruitment may

vary among years with different levels of recruitment. Additionally we have only measured recruitment from caches and not from other seed sources at the site. However we believe that at these sites the caches represent 95% of the seed rain for that year, and therefore the majority of recruitment measured at these sites was derived from caches. Further studies in which rats and all other introduced vertebrates were excluded from a site prior to flowering would be useful in providing information on natural seed dispersal and seedling recruitment. Since tussock grasslands are the main habitat of rats on Macquarie Island, we believe the distribution of rats will spread and overall numbers will increase with the predicted expansion of tussock grasslands (Copson & Whinam 2001). This will increase the potential for further impact on *P. hookeri*. Understanding the impact of this introduced species on the vegetation of Macquarie Island is important for proper management of this World Heritage site.

Chapter 7 – Final discussion and conclusions

Quantifying life history strategies of species occurring at the southern limit of vascular plant distribution enables us to understand selection pressure and consequently evolutionary processes. In order to understand biodiversity and speciation it is imperative to know how species are selected for within their environment. Subantarctic islands provide perfect models for studying such processes. These islands are principally closed systems with low immigration, the climate is extremely constant and anthropogenic influences a recent phenomena (less than three hundred years). There has been much debate over the description of the subantarctic climate. It is not appropriate to define it as harsh, as winter temperatures are much warmer than those of arctic taiga forests, nor are there permafrosts as in arctic tundra. The word "extreme" implies climate anomalies, or large climatic variations such as desert environments where it is hot by day and freezing by night, or polar deserts which are very cold and dry and its use in describe the subantarctic environment is anthropomorphism. The most biologically limiting climatic feature of the subantarctic environment, particularly on Macquarie I., is simply the constancy of low air temperatures. This coupled with strong winds and low sunlight due to constant cloud cover, results in an environment which is assumed to be challenging for plant growth. Yet given this *challenging* environment many plant species occur on these islands and most are productive.

Subantarctic islands are small, isolated land masses surrounded by ocean, and most including of Macquarie I. have never been attached to another land mass. This isolation creates another hurdle for the establishment of terrestrial organisms in the

subantarctic. The isolated nature of subantarctic islands prompts one to question 'how did the organisms that occur on the islands arrive there?' Chapter 2 discussed the role of long distance dispersal in the colonisation of Macquarie I. Additionally, that all islands have differing species richness poses the question 'what determines an island's species richness?' In a study on ecological biogeography of Southern Ocean islands, Chown et al. (1998b) investigated island biogeography by examining the relationship between island area and species richness. They found that indigenous vascular plant species richness on Southern Ocean islands was attributable to island area and temperature. Furthermore, these authors pointed out that the increase in species richness with increasing temperature is more rapid on temperate islands than on colder ones. Insect species richness was attributed to vascular plant species richness and distance to the nearest continent. Chown et al. (1998b) concluded that a Southern Ocean island's biota can be explained by conventional island biogeographic variables.

No two islands, despite similar size or proximity, have the same biota. Greve et al. (2005) presents the debate on biogeography of Southern Ocean islands; some choose to group the islands as single biogeographic province; while others provide a multi-regional view. By investigating nestedness of biotas across the region Greve et al. (2005) found that vagility had a marked influence on nestedness and the biogeographical patterns shown by indigenous species. Greve et al. (2005) identified that there was significant nestedness of the indigenous plant biota of the New Zealand Is, which included Macquarie I.

In the past plant many ecologists have examined plants growing in the Southern Ocean (or subantarctic) at a regional level and investigated plant strategies for growing in the subantarctic or cool temperate climate. It has been commonly stated

that plants in cold environments, such as alpine, high latitudes and the subantarctic, typically relied on asexual reproduction (Bliss 1971; Bliss 1979; Lewis-Smith 1984; Körner 1999). Callaghan and Lewis (1971) showed that low temperatures restricted plant growth while short growing seasons limited flowering development on South Georgia. In habitats that are typified by low temperatures and limited growing seasons, plant growth and reproduction are often limited, with species showing a range of adaptations, such as perennial life history, storage of resource between seasons, over-wintering floral primordia, seasonally intermittent flowering, self compatibility and auto deposition of pollen (Pickering 1997).

This study examined sexual reproduction across a wide range of plant functional groups, in the subantarctic environment. Contrary to generalisations indicating sexual reproduction is of minor ecological importance in the subantarctic (Lewis-Smith 1984), this study found that 72% of the vascular plant species on Macquarie I. exhibited sexual reproduction through flowering (Ch. 2). Furthermore, 62% of flowering plant species dispersed seed. Seed trap data showed that irrespectively of the community over half of the species in any given stand of vegetation dispersed seeds. At four of the eight sites over 70% of the standing vegetation dispersed seed into seed traps. Overall, the more abundant a species, the greater the likelihood of its occurrence in the seed rain. This study suggests that a species' abundance on the island may be related to its ability to produce and disperse seed. Several species (*Luzula crinita, Stilbocarpa polaris, Pleurophyllum hookeri, Agrostis magellanica*) were found to disperse large numbers of seeds. Where the three largest species on the island (*Poa foliosa, S. polaris* and *P. hookeri*) dominated the standing vegetation they also dominated the seed rain. Two species (*S. polaris* and *Uncinia hookeri*) were

identified as being able to disperse to sites where there were no adults, suggesting they are can disperse over several kilometers, being capable of intra-island dispersal.

Once propagules are dispersed, the next major life history stage is germination and the emergence of seedlings. This study showed that in a single year over a quarter of all flowering plant species were able to produce seedlings seven species of herb, two species of megaherb and three species of grass. From this it appears that successful sexual reproduction may be more significant than previous thought. Ecologists have long acknowledged the role of flowering, seed production, dispersal and seed germination as vital steps in plant species survival (Grime 1979; Caswell 1989; Begon et al. 1996; Silvertown and Charlesworth 2001; Castro et al. 2004) and species expansion (Castro et al. 2004; Silvertown 2004). This study has found that these processes are also significant in the subantarctic environment and while several researchers have investigate germination requirements (Dorne 1977; Bergstrom et al. 1997; Hennion and Walton 1997a; Hennion and Walton 1997b) this is the first study to examine sexual reproductive effort of the majority of a subantarctic island's flora.

Strong seasonal patterns of reproduction were apparent across all species, regardless of life form or taxonomy. Flowering occurred in late spring and summer, fruit formed by autumn, dispersal occurred during autumn and winter, while most seedlings did not begin to emerge until late summer (although for some megaherb populations seedlings emerged in July). The only species that flowered, dispersed and produced seedlings throughout the year was the alien species *Poa annua*. These seasonal patterns of various stage of life history traits across species suggests that climate influences the

timing of such events, as it is the only commonality amongst this diverse group of taxa.

This annual, seasonal reproductive pattern observed in most of the species studied does not appear to be replicated in other subantarctic islands. For example, this pattern was not found in *Festuca contracta,* a widespread subantarctic grass, on South Georgia. Tallowin and Smith (1977) reported that *F. contracta* exhibited floral induction and initiation in summer, while seed development and production was not completed until the following growing season. On South Georgia *F. contracta* reproduction is seasonal but has a different pattern in that it spans two seasons. This may attributable to the lower mean air temperature of South Georgia compared with Macquarie I., indicating that climate may be a significant factor affecting species reproductive performance. The implication is that climate change may have substantial impact on reproductive performance of subantarctic plants. This leads to the question will all species respond to changes temperature the same way?

In a detailed study of megaherbs biomass allocation and life history strategies were examined. The study (Ch. 3) found that despite extant climatic conditions of Macquarie I. megaherbs allocate considerable resources to sexual reproduction. The species have differing flowering strategies, *P. hookeri* allocated comparatively more biomass (18-42%) to flowering but only flowered every two to three years while *S. polaris* allocated 16-20% of total plant biomass to flowering and seed production each year.

P. hookeri allocated a greater proportion of reproductive biomass to pedicels enabling the small pappussed seeds to be lifted above the rosette, which aids wind and gravity dispersal. *S. polaris* however, produced peduncles resulting in the umbel inflorescence which is then able to be blown or roll, as observed. As shown in the seed rain experiment this enabled *S. polaris* seeds to be dispersed beyond its occurrence.

The study identified that these megaherbs can produce large quantities of seed for *P. hookeri* over 43, 000 seeds per plant and for *S. polaris* over 40, 000 seeds per plant. This large reproductive effort was also evident in seed rain with both species having high seed density; for *P. hookeri* over 13, 300 seeds m^{-2} and for *S. polaris* over 10, 000 seeds m^{-2}.

Megaherbs dominate the island's vegetation, with their large leaves and abundant large inflorescences in contrast to the surrounding vegetation. Despite low temperatures and low radiation, herbfields have a large standing crop. Jenkin and Ashton (1979) calculated that a Macquarie I. *P. hookeri* herbfield has twice the biomass of alpine herbfields from N.E. Victoria, Australia. Tweedie (2000) likened the productivity of coastal *S. polaris* herbfields to that of a tropical rainforest. However this study, for the first time, investigated the attributes of megaherbs as a functional group on Macquarie I. The biomass study (Ch. 3) quantified megaherb attributes, how they allocate resources and if this varied between the two species. The study found that megaherbs allocated 50% or more of their total biomass to leaf tissue.

The macrophyllous, megaherb growth form has evolved independently in number of diverse plant families in the subantarctic (Moore 1979; Mitchell et al. 1999). Mitchell

suggested it was the balance of available water and nutrients, constant temperature and absence of grazing mammals on subantarctic islands that lead to the evolution of the megaherb form. It is most probable that the ability to produce large amounts of photosynthetic leaf material enable megaherbs to overcome low light, wind damage and create a microclimate around the plant, enabling them to be established and widespread across the subantarctic. The study highlighted some differences between the species. *P. hookeri* allocated resources to lamina and not petioles, which results in a wide rosette habit, while *S. polaris* formed long petioles elevating lamina up off the ground. These differing strategies allow both species to out-compete other surrounding species.

Neither *P. hookeri* nor *S. polaris* dominate the vegetation of Campbell or Auckland Is. where mean temperatures are higher and species diversity greater. The dominance of *P. hookeri* and *S. polaris* of Macquarie I. vegetation reflects the absence of other large competitive species.

Significant differences were found between the Macquarie I. megaherbs growing across different environments. It was expected that plants would perform differently at different altitudes as other studies have shown (Tweedie 2000, Jenkin 1972). *S. polaris* plants growing at a higher altitude were smaller and allocated less resources to the rhizome and more to leaf tissue. This may indicate that the plants were stressed and therefore unable to allocate surplus resources to the rhizome which acts as a storage organ. The influence of altitude was not as clear cut for *P. hookeri* which has a wider altitudinal amplitude. It appeared that waterlogging, nutrient availability and rabbit grazing also had an impact on *P. hookeri* growth. The smallest plants were

produced at a high altitude exposed site on mineral soils and a low altitude waterlogged herbfield. It was difficult to determine why the largest plants occurred at a south-west facing, mid-altitude herbfield. Perhaps it was the free draining soils or the long history of reduced rabbit populations due to myxomatosis infections at the site. Further studies are needed to identify nutrient and microclimate requirements for *P. hookeri.*

There was a 98% chance of seedlings emerging from naturally dispersed seed aggregates for *P. hookeri* and *S. polaris.* Most seeds stayed dormant during winter emerging in early spring. Such seasonal germination provided newly emerged seedlings a longer photoperiod and potentially more light as canopies had not yet expanded to their maximum summer extent. The study found there was a significant reduction in seedling density from spring to summer. The seedling densities recorded within plots were some of the highest seedling densities measured for high latitude or alpine herbfield communities (Cooper et al. 2004). Both species had high maximum seedling densities; for *P. hookeri* 1791 m^{-2} and for *S. polaris* 688 m^{-2}. The study also identified significant inter-population variation in seedling densities. Given that biomass values showed that reproductive effort varies with population, it is likely site conditions (ie. microclimate, nutrients) strongly influence reproductive output and consequently recruitment.

Many megaherb seedlings began dying during summer. Drought, leaf deposition, herbivory (native and introduced species) and physical disturbance were identified as potential causes of this mortality. It is difficult to determine the specific impact of each of these attribute. However, there was much microsite variation with an entire

plot (20 cm x 20 cm) of seedlings undergoing 100% mortality, whilst adjacent plots (< 2 m away) had high seedling survivorship, and even within plots some seedlings survived while others died. Overall, megaherb seedling densities were high in early summer but by late autumn most seedlings had died.

Despite previous plant functional and physiological studies in the subantarctic environment very little is known of their life history traits. Demographic studies (Ch 5.) utilising stage transition matrices identified that *P. hookeri* populations were dominated by mature plants with high survivorship. In such a stable environment where disturbance, immigration and competition are low, this was hardly surprising. The study identified that in general, low levels of recruitment do occur through seedlings. Stable populations of old plants, maintained by vegetative reproduction have low genetic diversity as vegetative reproduction offers little opportunity for gene flow between individuals. The emergence of new individuals via sexual reproduction (ie. seeds) may maintain some degree of genetic diversity within populations, particularly those that are geographically isolated with limited immigration, (if pollination was due to selfing, genetic diversity would not necessarily be increased, however wind is considered to be the most likely vector of pollination for *P. hookeri*). Additionally seeds facilitate dispersal allowing populations to expand, and in some cases (Ch. 2) move beyond their present distribution.

Recruitment into populations was disproportionately low to the amount of seed and seedlings produced, due to the high mortality observed. Recruitment levels varied between populations with plants growing at marginal sites (identified by low biomass and reproductive output) having the lowest incidence of seedling recruitment in the populations. Marginal sites were either high in altitude and therefore, exposed, low

nutrient environments (and in some cases coupled with rabbit grazing pressure.) However, at one low altitude, waterlogged, low nutrient site, recruitment was attributable to vegetative reproduction only. From this inter-population variation in recruitment it can be concluded *P. hookeri* population dynamics and specifically recruitment varies with environmental conditions.

Overall *P. hookeri* populations were dominated by adult plants with few juveniles recruiting into the population, so why do they produce so much seed? *P. hookeri* possesses the following attributes (as per Convey 1996a); long-lived, highly competitive, efficient resource capturing, iteroparity, the ability to vegetatively reproduce and low juvenile survivorship. Forbis and Doak (2004) stated that low seedling survivorship in alpine perennials was not due to the environment influencing survival dynamics, but merely the predicted pattern of long-lived species. They stated while the alpine environment can strongly shape life history it does not appear to alter the shape or strength of life history trade-offs. Low seedling survival for such a long-lived plants is not necessarily detrimental, the study has shown that population structures have evidence of establishment events possibly separated by decades, which highlights the need for further long-term monitoring.

It is difficult to accurately quantify environmental parameters such as moisture availability, exposure, snow cover, wind abrasion, historical and current grazing pressure across numerous widespread sites without substantial funds and resources, and therefore was beyond the scope of this study. Future studies should attempt multivariate analysis of the population attributes across environment parameters. Due to logistic constraints megaherb tissue samples collected for nutrient analysis (total nitrogen) from each population were not able to be processed. Further studies

examining such properties will provide some indication of plant performance and vigour over differing environments. Multivariate analysis of these parameters and seedling survivorship would assist in further identifying the determinants of megaherb recruitment. Further studies excluding all but one parameter may indicate the influence of these parameters on megaherb seedling survivorship, for example, insecticide application to eliminate invertebrates, such as slugs, from seedling plots (as per Bevill et al 1999) or supplementary watering to reduce drought. Quantifying the impact of microclimate attributes such as freeze-thaw cycles and soil drying, will also assist in understanding the impacts of climate change on megaherb population growth and viability.

Both Macquarie I. megaherb species are clonal, and the presence of vegetative clones would be a useful strategy to conserve energy in this low-energy environment. Yet megaherbs appeared to produce an over abundance of seed. The study has shown that this high resource allocation to sexual reproduction is a successful strategy. In assessing the species life history strategies and function Convey (1996b) concluded that *Deschampsia antarctica,* which is widespread occurring on many islands and continents, presence in Antarctica was most likely due to chance colonisation rather than any specific functional strategies.

By producing vast amounts of seed both *P. hookeri* and *S. polaris* there is an increased chance that some seedlings survive to become juvenile plants, despite high seedling mortality. Is the massive reproductive effort in megaherbs the legacy of a species evolved from a more variable environment, where seedling survivorship is greater but populations less stable or is it an evolutionary legacy of ancestors to the

Apiaceae and Asteraceae family, both of which are known to be prolific seed producers? Or, megaherbs may have been selected for by stochastic events such as landslips, simply because they produce so many propagules which are important in community succession following such events.

This is the first study to quantify the impact of rats on a megaherb species, although the degree of rat impact on *S. polaris* population recruitment through seed predation remains unquantified. Rats affected seed dispersal by constructing unnaturally dense seed piles, and once excluded from these seed piles were shown to impact on initial seedling survivorship. The study found that after 18 months rats had little impact on long term seedling survivorship as most seedlings died regardless of rat access or not. However, the high mortality documented throughout this study may have been due to an unquantifiable environmental variable or possibly slug herbivory on older, larger seedlings. For this reason long-term monitoring is essential for understanding plant population recruitment.

The deleterious impact of introduced species on the terrestrial subantarctic environment has been documented for the subantarctic region (Frenot et al. 2005). Of all the southern ocean islands only Heard I. remains devoid of introduced terrestrial vertebrates and this study (Ch. 6) further highlights the need to maintain stringent quarantine procedures and protocols. As subantarctic megaherbs occur on only a few southern oceanic islands, (ie. they are not widespread across all islands) they are extremely vulnerable to extinction. On Campbell and Auckland Is. both species of megaherb have been drastically reduced as result of sheep and rabbit grazing.

For almost fifty years researchers have been highlighting the negative impacts of rabbits on the Macquarie I. ecosystem (Carrick 1957; Costin and Moore 1960; Copson et al. 1981; Selkirk et al. 1983b; Brothers and Copson 1988; Scott 1988; Copson and Whinam 1994) and with this study being no exception, rabbits are deleterious to megaherb growth, reproduction and recruitment. Yet at the time of writing rabbits appear to be increasing, from numbers seen in the late 1980s post-myxomatosis introduction. This is likely to be due to the apparently milder winters, rabbit population resistance to the myxoma virus and absence of cats (pers. comm. Copson), and it is likely that general climate change (Tweedie and Bergstrom 2000) is having an influence. If eradication is not undertaken in the near future, the island's vegetation will be severely compromised in a many ways, and may never recover. Species endemic to the island, such as the orchid (*Nematocerus dienema*) may become extinct. The vegetation of Macquarie I. is significant in terms of global biodiversity, as it supports the largest and most intact populations of these restricted subantarctic megaherbs, *S. polaris* and *P. hookeri.*

The findings of this study dispelled the myth that plants in the subantarctic do not rely on sexual reproduction. The majority of the island's plant species flowered during the study, many produced seeds with some producing seedlings. The results indicate that subantarctic plants do produce and disperse viable seed and that seedlings are recruited into populations. For *P. hookeri*, the rate of sexual recruitment often exceeds asexual recruitment. Megaherb growth form dominates some vegetation types on several subantarctic (or Southern Ocean islands) islands. The two species studied (*P. hookeri* and *S. polaris*) only occur in the Southern Ocean island environment, on Macquarie I. and three nearby islands (island archipelagos). The Macquarie I. populations of *P. hookeri* and *S. polaris* represents the southern limits of both species.

To study the life history traits of these unusual growth forms in the subantarctic helps us to understand how the environment has selected these species, and consequently helps us to further understand the processes of evolution.

Following on from this work there remains much scope for further studies on subantarctic terrestrial ecology. Of particular note is the needed for studies on pollination biology, seed viability, seed and seedling predation and further quantification of microclimate. Future studies on subantarctic terrestrial ecology should be integrated investigations across several Southern Ocean islands which have similar functional groups and climates, examining shared taxa or shared habit.

This study highlights the importance of a multidisciplinary approach when investigating plant ecology. The initial design of this project did not aim to investigate the role of introduced species on plant recruitment and survival, however, as the study progressed, it became apparent that introduced species were altering ecosystem dynamics and specifically plant recruitment and survival. The findings of this thesis also indicate the importance of extended regular field work, as seasonal trends were observed over 17 continuous months spent on Macquarie I. Furthermore, the importance of longer term studies were reinforced by revisiting the island in March 2002 (28 months after the study commenced) where seedling survivorships were found to be different from earlier results in March 2001. This study also shows that when studying plant attributes it is important to monitor a species or community over a range of different environments, as plant performance can vary over climatic gradients. Given that demographic variation was observed in populations across sites of differing climate, there are implications that climate change will alter population

recruitment and thus population sustainability. Ongoing monitoring is imperative to effectively manage and conserve Southern Ocean islands, and further our understanding of terrestrial plant ecology.

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Appendices

Appendix 1. Species List of the Vascular Flora of Macquarie Island.

The 44 vascular plant species that occur on Macquarie Island are listed below (after (Hnatiuk 1993; Jones et al. 2002). Author citations follow Brummitt and Powell (1992).

PTERIDOPHYTES

Dryopteridaceae

Polystichum vestitum (G. Forst.) C. Presl

Blechnaceae

Blechnum penna-marina (Poir) Kuhn

Grammitaceae

Grammitis poeppigiana (Mett.) Pic. Serm.

Hymenophyllaceae

Hymenophyllum falklandicum Baker

Lycopodiaceae

Huperzia australiana (Herter) Holub

ANGIOSPERMS: DICOTYLEDONS

Apiaceae

Azorella macquariensis Orchard

Hydrocotyle novae-zeelandiae DC.

Stilbocarpa polaris (Hombr. et Jacquinot ex Hook. f. A. Gray)

Asteraceae

Leptinella plumosa (Hook. f.) Hook. f.

Pleurophyllum hookeri Buchanan

Brassicaceae

Cardamine corymbosa (Hook. f.) Allan

Callitrichaceae

Callitriche antarctica Engelm. ex Hegelm.

Caryophyllaceae

Cerastium fontanum Baumg. subsp. *fontanum*

Colobanthus muscoides Bartl

Colobanthus affinis (Hook.) Hook. f.

Colobanthus apetalus (Labill.) Druce var. *alpinus* (Kirk) L. B. Moore

Stellaria decipiens Hook. f.

Stellaria media (L.) Cirillo

Crassulaceae

Crassula moschata G. Forst. f.

Haloragaceae

Myriophyllum triphyllum Orchard

Onagraceae

Epilobium brunnescens (Cockayne) P. H. Raven et Engelhorn subsp. *brunnescens*

Epilobium pedunculare A. Cunn.

Portulacaceae

Montia fontana L. subsp. fontana

Ranunculaceae

Ranunculus crassipes Hook. f.

Rosaceae

Acaena magellanica (Lam.) Vahl

Acaena minor (Hook. f.) Allan

Rubiaceae

Coprosma perpusilla Colenso ssp. *subantarctica* Orchard

Galium antarcticum Hook. f.

ANGIOSPERMS: MONOCOTYLEDONS

Cyperaceae

Carex trifida Cav.

Isolepis aucklandica Hook. f.

Uncinia divaricata Boott

Uncinia hookeri Boott

Juncaceae

Juncus scheuchzeroides Gaudich.

Luzula crinita Hook. f. var. *crinita*

Orchidaceae

Nematoceras dienema (D. L. Jones) D. L. Jones, M. A. Clem., & Molloy

Poaceae

Agrostis magellanica Lam

Deschampsia caespitosa (L.) B. Beauv.

Deschampsia chapmanii Petri

Festuca contracta Kirk

Poa annua L.

Poa foliosa (Hook. f.) Hook. f.

Poa cookii (Hook. f.) Hook. f.

Poa litorosa Cheeseman

Puccinellia macquariensis (Cheeseman) Allan & Jansen

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Skotnicki, M., Selkirk, P., Kitajima, E., McBride, T., Shaw, J., Mackenzie, A., 2003. The first subantarctic plant virus report: Stilbocarpa mosaic bacilliform badnavirus (SMBV) from Macquarie Island, Polar biology, 26(1), 1-7